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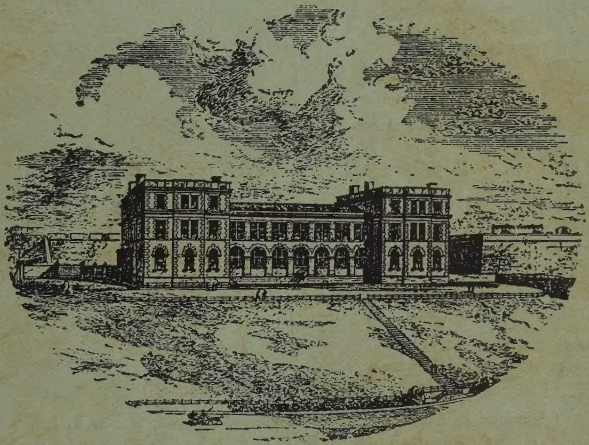

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The Seasonal Abundance and Distribution of the Pelagic Young of Teleostean Fishes Caught in the Ring-trawl in Offshore Waters in the Plymouth Area. Part II.

By

F. S. Russell,

Naturalist at the Plymouth Laboratory.

With 8 Figures in the Text.

A REPORT was published in 1930 on the seasonal abundance of young fish in the plankton covering the years 1924 to 1929 (Russell, 1930, b). On concluding that report it was thought that for several reasons it would be worth while continuing the routine weekly collections on the standard basis of half-hour oblique hauls with the 2-metre stramin ring-trawl for a further period of years.

During the compilation of the 1930 report there was a constant desire to know what the composition and abundance of the young fish fauna might have been in past years, but no data of a sufficiently quantitative and comparable nature were available. The 1930 report was based on a series of collections not all of which had been taken in the same way, and in no year were collections made continuously throughout the twelve months. It was therefore thought advisable that a series of collections all made in the same way should be obtained regularly through the twelve months for a number of years in succession. Thus there would be formed a standard set of data to act as a basis for comparison for those who may come after. It is only by such methods that it will be possible to observe faunistic changes over a very long period of years.

We want also to know to what extent a planktonic population of young fishes comprising some fifty or more species varies in its proportional composition from year to year. It was thought that in a population of so many species of fishes there would be found evidence of those violent fluctuations in abundance that bring about the well-known good and bad survival years which so vitally affect the composition of our food-fish stock. In the event of such fluctuations appearing it would be interestng to observe whether a good or bad year for one species of fish held good also for certain other species whose young occurred in the plankton at the same time of the year. Under such circumstances if a number of species were affected in the same way in one year it might be found possible to obtain indications of some of the causes of fluctuations.

The collections, 220 in all, were made (with 4 exceptions, see footnotes to Table III) at a position 2 miles east of the Eddystone lighthouse in water of a depth of about 54 metres. They are therefore indicative of offshore conditions. For a work of this nature to be complete it is necessary to know the spawning areas of the different species of fish; unfortunately our knowledge is largely lacking in this respect. It is thought, however, that even if the centre of a spawning area is situated at some distance, an increase or decrease in abundance would show itself in outlying regions among those species whose pelagic young normally occur in the waters off Plymouth. It must, however, always be borne in mind that a change in abundance thus shown may be produced by a shifting of the normal spawning area. But when the young of any species are present normally in large numbers there is some justification for believing that a large body of adult fish must have been spawning in waters at no great distance from Plymouth, or at any rate that the spawning area is so situated that it is normal for a large number of the fry produced to drift past in our offshore waters.

The collections were made in the stramin ring-trawl (diameter at mouth, 2 metres; length, 6 metres; stramin obtained from Messrs. N. P. Utzon, Copenhagen, *ca.* 16 strands to one inch) by means of oblique hauls. A description of the method of working has already been given (Russell, 1930, a, p. 640) the net being first fished at the surface and then in successive steps with 10, 20, 35, 45 and 60 fathoms of wire out respectively, so that the net was in the water for half an hour. The net was fished on the warp used for the otter trawl and collections were made by the crew of S.S. *Salpa* under the supervision of Capt. V. Lord. As nearly as possible the collections were taken at weekly intervals, and they cover the years 1930 to 1934 inclusive.

It may be thought that material obtained by only a single collection each week is insufficient to base conclusions on; the results have on the whole, however, shown such consistency that they seem to prove their own reliability.

In collections of this sort weather conditions under which the work is undertaken should be considered. There is of course a limit in wind and sea conditions beyond which it is impracticable to work the gear. A few of the collections have, however, been made under conditions when it was found necessary to use a four-inch dredge-rope, rather than the wire trawl warp, for fear of the sudden jerks on the less elastic wire straining unduly the meshes of the stramin. Since collections were made in weather conditions up to this limit, the relations between the size of the catches and the wind force under which they were obtained have been examined. It was, however, found that just as large catches were likely to be taken on rough days as on calm and that on the whole weather conditions were not likely to have upset the true picture of the results. It is only natural that whenever possible the most suitable days were chosen for collecting.

The data obtained are here given in a similar manner to that adopted in the previous report. The average catches per half-hour haul for each month in each year of all fishes combined and of the post-larvæ of each species are given in Table IV* on page 176. By adding these averages for any one month and dividing by the number of years in which collections were made in that month an average monthly catch was obtained for the period of the five years 1930 to 1934 inclusive. These average catches are given in Table I. In the last two columns of Table I are also given the sums of these average monthly catches for 1930 to 1934, and for 1924 to 1929 from Table I, page 712, of the 1930 report.

The dates in each year on which the collections were made are given in Table III on page 175.

GENERAL RESULTS.

In considering the data obtained it is firstly of interest to gain an idea of the general picture of the abundance at different times of the year of all species of fish combined. In doing this the Clupeids have been excluded owing to the possibility that daylight figures do not give a true picture of their abundance (Russell, 1930, a, p. 649), and also because on account of the shoaling habits of the spawning fish the results are occasionally distorted by the occurrence of large numbers of newly hatched larvæ in the plankton. Accordingly in Table IV (p. 176), besides the average monthly catches in each year of all fish combined, corresponding figures are also given for all fish excluding Clupeids. By adding together the average monthly catches of the latter and dividing by the number of years, average figures can be obtained for the five-year period, 1930 to 1934, which give a mean picture of the seasonal occurrence and abundance of the fish in the collections. But there is a possibility that by grouping the catches into calendar months a slightly distorted picture of the true sequence of events might be produced if at any time the greatest catches of fish appeared either near to the beginning or the end of a month. The months have accordingly been subdivided into fortnightly periods, so that those catches falling on the 1st to the 15th day of the month inclusive have been included in the first fortnight and those on the 16th to the last day of the month in the second fortnight. The data so obtained have been plotted in the form of a graph in Figure 1. The curve shows clearly that the maximum abundance of young fish may be expected to occur during the period between the second fortnight in April and the first fortnight in June. In June the numbers in the catches fall off considerably and a period of low productivity lasts from then until the first fortnight in September, after which the young fish almost die out

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* In this table when the average for the month is less than 0·5 a + has been inserted.

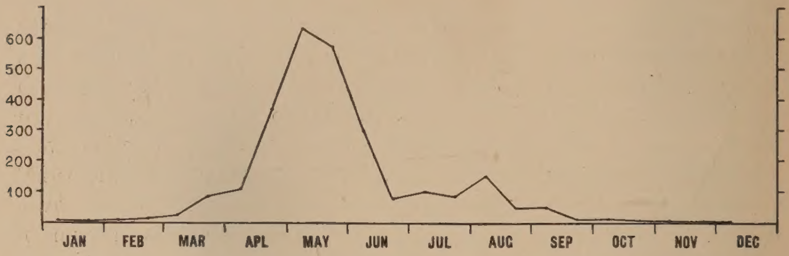

Fig. 1.—Curve showing the average catches in half-hour oblique hauls with the 2-metre ring-trawl for each fortnight for all young fish, excluding Clupeids, averaged over the whole period 1930 to 1934 inclusive.

from the collections. This curve in Figure 1 may be regarded as a type of mean seasonal distribution to be used as a standard with which the distributions in any individual year may be compared. That this may be regarded as a reliable mean gains support from a comparison with the results obtained during the previous period, 1924 to 1929. The curves

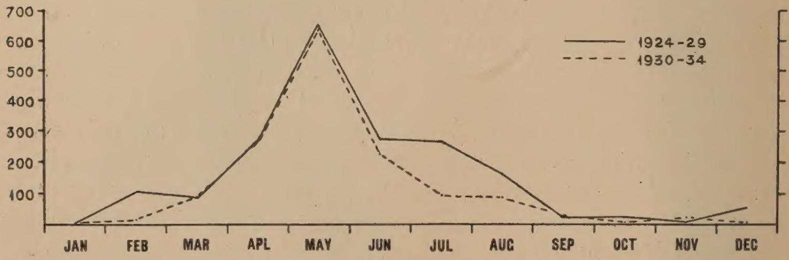

Fig. 2.—Curves showing the average monthly catches in half-hour oblique hauls with the 2-metre ring-trawl for all young fish, excluding Clupeids, for the two periods 1924 to 1929, and 1930 to 1934 inclusive.

for the average monthly catches for the two periods 1924–29 and 1930–34 have been drawn in Figure 2. The agreement between these two curves is remarkably close, the only anomalies being in February, which month in the former period is based on collections in one year only (1928) when there was a heavy catch of very small Ammodytes post-larvæ, and in July and August when the 1924–29 totals appear to have been significantly higher than those for 1930–34 (see p. 169).

THE SEASONAL COMPOSITION OF THE CATCHES.

Before proceeding with a comparison of the individual years, it will be well to analyse the curve in Figure 1 to find out what species are responsible for the general shape of the curve and how the composition of the catches varies with the time of year. In the previous report (1930, p. 711) a table is given showing the months in which the maximum abundance of the post-larvæ of each species may be expected on the average. The results in Table I, p. 712, of the 1930 report have been combined with those given in Table I of this report, and a new table has been produced showing the months in which each species may be expected to occur in maximal abundance averaged over the eleven years, Table II. When examining this table it should be remembered that when two fish fall in the same month their actual seasonal distribution may be slightly different, one species having a bias towards the previous month and the other to the succeeding month. Table I should therefore be used in conjunction with Table II as it gives a truer picture of the average seasonal distribution. When a species only occurs in very small numbers over a number of months the month in which the greatest numbers have been taken on the whole period has generally been chosen for insertion in Table II. In constructing this table an attempt has also been made to assign each species to its geographical area. Divisions have been made on the basis of Hjort's data (1910, p. 442 *et seq.*) in which he has divided fish into northern and southern species. In making this division one has to realise that the distinction is not one of latitude only but that the distribution of the temperature of the water must also be taken into consideration. In Table II Hjort's northern species have been designated boreal, and these species have been further subdivided into those whose distribution tends towards arctic-boreal regions, those which are centred about the North Sea, and those species whose distribution tends towards the waters of the south-west of the British Isles. These three divisions are indicated in Table II by the letters N, B, and S respectively after the names of the fish. Hjort's southern species are here regarded as warm-water species, and these have again been further subdivided into those species whose centre of distribution tends towards the northerly boundary south-west of the British Isles and follows the warm water up the west coasts of the British Isles, and those which tend to be even more southerly in character. These last two divisions are indicated by the italicised letters *N* and *S* respectively after the names of the fish in question. The two main divisions, boreal and warm water, are also indicated in Table II by printing the boreal species in roman type and the warm-water species in italics. Some difficulty was experienced in assigning the different fish to their respective areas, since it is their abundance in different localities

TABLE I.

Average Monthly Catches of Post-larvæ per Half-hour Oblique Haul with 2–metre Ring-trawl, 1930–1934.

	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Totals. 1930–34.	Totals. 1924–29.
Clupeid spp.*	72	227	491	87	56	35	23	25	14	72	16	4	1122	379
Gadus pollachius	–	–	+	2	10	+	–	–	–	–	–	–	12	11
Gadus merlangus	–	–	2	65	109	19	1	+	–	–	–	–	196	131
Gadus minutus	–	2	40	28	25	+	–	–	–	–	–	–	95	124
Gadus luscus	4	3	2	2	3	+	+	1	–	2	4	1	22	82
Gadus callarius	–	+	+	+	–	–	–	–	–	–	–	–	+	1
Onos spp.†	–	–	1	16	30	5	+	–	–	+	+	–	52	30
Molva molva	–	–	–	–	1	1	–	–	–	–	–	–	2	8
Merluccius merluccius	–	–	–	–	–	+	–	+	+	+	–	–	+	3
Raniceps raninus	–	–	–	–	–	–	+	+	–	+	–	–	+	+
Capros aper	–	–	–	–	–	–	+	+	+	–	–	–	+	1
Zeus faber	–	–	–	–	–	–	–	+	+	+	–	–	+	+
Arnoglossus spp.‡	–	–	–	–	–	1	4	10	17	1	+	–	33	33
Rhombus lævis	–	–	–	+	+	+	+	+	+	–	–	–	+	
Rhombus maximus	–	–	–	–	–	+	+	1	+	–	–	–	1	5
Scophthalmus norvegicus	–	–	+	8	32	17	2	+	–	–	–	–	59	60
Scophthalmus unimaculatus	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Zeugopterus punctatus	–	–	–	2	3	1	–	–	–	–	–	–	6	9
Pleuronectes limanda	–	–	3	17	40	5	–	–	–	–	–	–	55	83
Pleuronectes flesus	–	–	1	2	2	+	–	–	–	–	–	–	5	6
Pleuronectes microcephalus	–	–	1	1	15	6	+	–	–	–	–	–	23	33
Solea vulgaris	–	–	1	2	2	+	–	–	–	–	–	–	5	6
Solea variegata	–	–	+	13	45	24	1	+	–	–	–	–	83	79
Solea lascaris	–	–	–	–	–	–	+	+	+	+	–	–	+	1
Serranus cabrilla	–	–	–	–	–	–	–	+	1	–	–	–	1	1
Caranx trachurus	–	–	–	–	–	–	1	8	5	+	–	–	14	44
Mullus surmulletus	–	–	–	–	–	–	+	+	–	–	–	–	+	+
Morone labrax	–	–	+	+	+	–	–	–	–	–	–	–	+	+
Ammodytes tobianus**	2	4	19	2	+	+	+	+	+	+	–	–	27	116
Ammodytes lanceolatus	1	+	+	4	9	4	2	4	+	+	–	–	24	57

Cepola rubescens	–	–	–	–	–	–	–	+	+	–	–	–	+	1
Callionymus spp.§	–	+	11	76	301	104	28	22	2	3	1	+	548	965
Labrus bergylta	–	–	–	–	1	2	+	–	–	–	–	–	3	12
Labrus mixtus	–	–	–	–	+	1	–	–	–	–	–	–	1	8
Ctenolabrus rupestris	–	–	–	–	–	1	9	4	+	–	–	–	14	20
Crenilabrus melops	–	–	–	–	–	+	1	+	–	–	–	–	1	6
Centrolabrus exoletus	–	–	–	–	–	–	1	+	–	–	–	–	1	4
Trachinus vipera	–	–	–	–	–	–	3	4	+	–	–	–	7	22
Trachinus draco	–	–	–	–	–	–	–	+	–	–	–	–	+	+
Scomber scombrus	–	–	–	–	–	10	9	3	+	–	–	–	22	29††
Gobiid spp.	+	+	+	+	3	6	15	19	+	+	+	+	43	145
Lebetus scorpioides	–	–	–	–	–	+	+	1	1	+	–	–	2	16
Blennius pholis	–	–	–	–	+	–	+	+	–	–	–	–	+	2
Blennius ocellaris	–	–	–	–	–	–	+	2	1	–	–	–	3	1
Blennius gattorugine	–	–	–	–	+	+	9	3	+	–	–	–	12	15
Chirolophis galerita	+	2	5	+	–	–	–	–	–	–	–	–	7	6
Agonus cataphractus	–	–	–	+	–	–	–	–	–	–	–	–	+	1
Trigla spp.¶	–	–	–	1	5	3	3	3	1	+	–	–	16	41
Cottus bubalis	–	+	3	2	1	–	–	–	–	–	–	–	6	8
Liparis montagui	–	–	+	+	+	+	–	–	+	–	–	–	+	3
Lepadogaster bimaculatus	–	–	+	–	+	–	+	1	+	–	–	–	1	6
Lophius piscatorius	–	–	+	1	–	+	1	–	–	–	–	–	2	2
All young fish	78	238	582	329	696	259	116	112	43	79	21	6	2559	2256
Ditto less Clupeids	6	12	91	242	639	224	93	87	29	7	6	1	1437	1867

* Includes *Clupea harengus*, *C. sprattus*, and *C. pilchardus*.
† Includes mostly *Onos mustela* and *O. tricirratus*.
‡ Includes probably mostly *Arnoglossus laterna* and a few *A. imperialis* and *A. thori*.
§ Mostly *Callionymus lyra* in the spring, and some *C. maculatus* in summer.
¶ Includes *Trigla gurnardus*, *T. hirundo*, *T. cuculus*, and *T. lineata*.
†† Excluding 1926.
** The identification of Ammodytes post-larvæ is uncertain now that Raitt (1934) has raised a new species, *A. marinus*.

TABLE II.

MONTHS IN WHICH POST-LARVÆ OF DIFFERENT SPECIES MAY BE MOST ABUNDANT IN THE RING-TRAWL CATCHES.

(N., northern boreal; B., Boreal; S., southern boreal; *N.*, northern warm water; *S.*, southern warm water. Boreal spaces are printed in roman type: warm water species in italics.)

January.	March.	April.	May.	June.	July.	August.	September.	October.	December.
C. harengus B.	C. sprattus S. G. callarius N.	G. minutus B.	G. pollachius S. G. merlangus B.		*C. pilchardus N.*				*G. luscus N.*
			Onos spp. B. S.*	Molva molva B.	R. raninus B.			*M. merluccius N.*	
						C. aper S. *Z. faber N.*	*Arnoglossus spp. N. & S.*†		
		P. flesus B.	R. lævis B. S. norvegicus B. Z. punctatus B. P. limanda B. P. microcephalus B.	*S. unimaculatus N.*	R. maximus B.				
		S. vulgaris S. *Morone labrax N.*	*S. variegata N.*		*S. lutea N.*	*S. lascaris ? S.*	*S. Cabrilla S.*		
						C. trachurus S. *M. surmuletus S.*			
	A. ? tobianus N.		A. lanceolatus B.						
			C. lyra S.			*C. rubescens S.*			
				L. bergylta S. L. mixtus S.	C. rupestris S. C. melops S. C. exoletus S.				
						T. vipera S.			
	C. galerita N.			B. pholis B.	S. scombrus S. Gobiid spp.	L. scorpioides S. *B. ocellaris N.*			
				Trigla spp. B.S.‡	*B. gattorugine N.*				
	C. bubalis B. A. cataphractus N.								
			L. montagui N.						
				L. bimaculatus S. L. piscatorius S.					

* Onos mustela B.
Onos tricirratus S.

† *Arnoglossus laterna N.*
A. imperialis S.

‡ Trigla gurnardus B.
T. hirundo, cuculus and lineata S.

rather than the extreme known limits of their distribution that is of importance here. Hjort (1910, pp. 441–442) has given tables showing the percentage landed in each area of the total quantity landed for a number of species of food fishes; it is really this type of information that is required, and this is naturally not available for non-commerical species. The geographical distributions indicated in Table II must not therefore be regarded as final; in the main, however, it is probable that they are correct.

This table shows the general tendency for the colder-water species to appear earlier in the year and then their gradual giving way to warmer-water species which predominate in the summer months. But while there is this general sequence there is not strict adherence to the rule, since we may find southern boreal species appearing before northern boreal ones, and northern warm-water species before boreal forms. If, however, we examine closely-related species we find that the sequence is more strictly adhered to. The position of the Clupeids and of the soles, for instance, is distinctly early compared with the main body of species; yet the most northerly species of the Clupeids, the herring, occurs before the sprat, and the latter before the pilchard. Similarly *Solea vulgaris*, *S. variegata*, and *S. lutea* and *S. lascaris* follow one another in accordance with their geographical distribution from north to south. We thus see that among all species taken together there is, as we should expect, variation in time of abundance, i.e. all boreal species do not appear together and so on. But when we confine ourselves to nearly related species, the season of abundance of one species considered in relation to that of another is an indication of their relative geographical distributions. Schmidt has drawn attention to this fact for Gadoids (1909, pp. 154–155), and also species of Agonus and Cottus. An apparent exception to this rule may be found in the turbot, *R. maximus*, and the brill, *R. lævis*. Of these two the brill has perhaps the more southerly distribution, but breeds first. The turbot, however, is a rather deeper-water fish.

Tables I and II thus show us the composition of the young fish fauna at different times of the year which combine to produce the general curve of seasonal distribution given in Figure 1.

Comparison of this figure and the tables shows that although there are no more species appearing in the spring than in the summer, yet during the period April to June there are very many more young fish than in the later months. It will be of interest to see which species of fish produce this noticeable peak in the curve in the spring months. Accordingly the proportions of the more important species expressed as percentages of the total number of fish (excluding Clupeids) are given below for the months April, May, and June.

	April.	May.	June.
G. merlangus	24·7	17·1	8·5
G. minutus	10·6	3·9	–
Onos spp.	6·1	4·7	2·2
S. norvegicus	3·1	5·0	7·6
P. limanda	6·5	6·3	2·2
P. microcephalus	0·4	2·3	2·7
S. variegata	5·0	7·0	10·7
C. lyra	29·0	47·1	46·5

This shows that the two species of outstanding importance are *Gadus merlangus* and *Callionymus lyra*, and that the latter in May and June forms nearly half the catch of young fish. When these two species are subtracted from the remaining species of fish the spring peak in the curve in Figure 1 is largely flattened out. Yet there still remain a slightly greater number of fish in these months than in the later months. This fact, taken in conjunction with preponderance of boreal species to warm-water species shown in Table II, indicates that conditions may perhaps be regarded as slightly more favourable here for the spawning of northern fish as opposed to more southern species. It is, however, evident that this region lies very near the boundary between the two main divisions.

While in this seasonal succession almost all species show a definite seasonal periodicity in abundance, *Gadus luscus* and *Clupea pilchardus* show somewhat unorthodox habits. The young of *G. luscus* may be found in small numbers in almost any month of the year. In Table II its maximal month is given as December ; this position was caused by one very large catch in December, 1927. It appears that apart from this catch the species mainly occurs between January and May. It is a fish of somewhat unusual geographical distribution, being mainly centred around the Channel, south-western and western shores of the British Isles, and the French coast in the Bay of Biscay. The above period for the occurrence of post-larvæ of *G. luscus* has been shown also by the work of Schmidt (1910) and of Chevey (1929).

Clupea pilchardus is another species which appears to have a very extended spawning period. Large numbers of pilchard eggs have been found in April, 1924 and 1925, July, 1924 and 1926, September, 1926 and 1934, October, 1932 and 1933, November 1930 and 1933, and December, 1931. It is likely, therefore, that any Clupeid occurring after the increase of sprat in February, March, and April, will be pilchard right up to the end of the year when young herring begin to appear in December.

The post-larval stages of Ammodytes also occur during many months of the year, but now that Raitt (1934) has shown the occurrence of a third species, *A. marinus*, the identification of *A. tobianus* may be wrong.

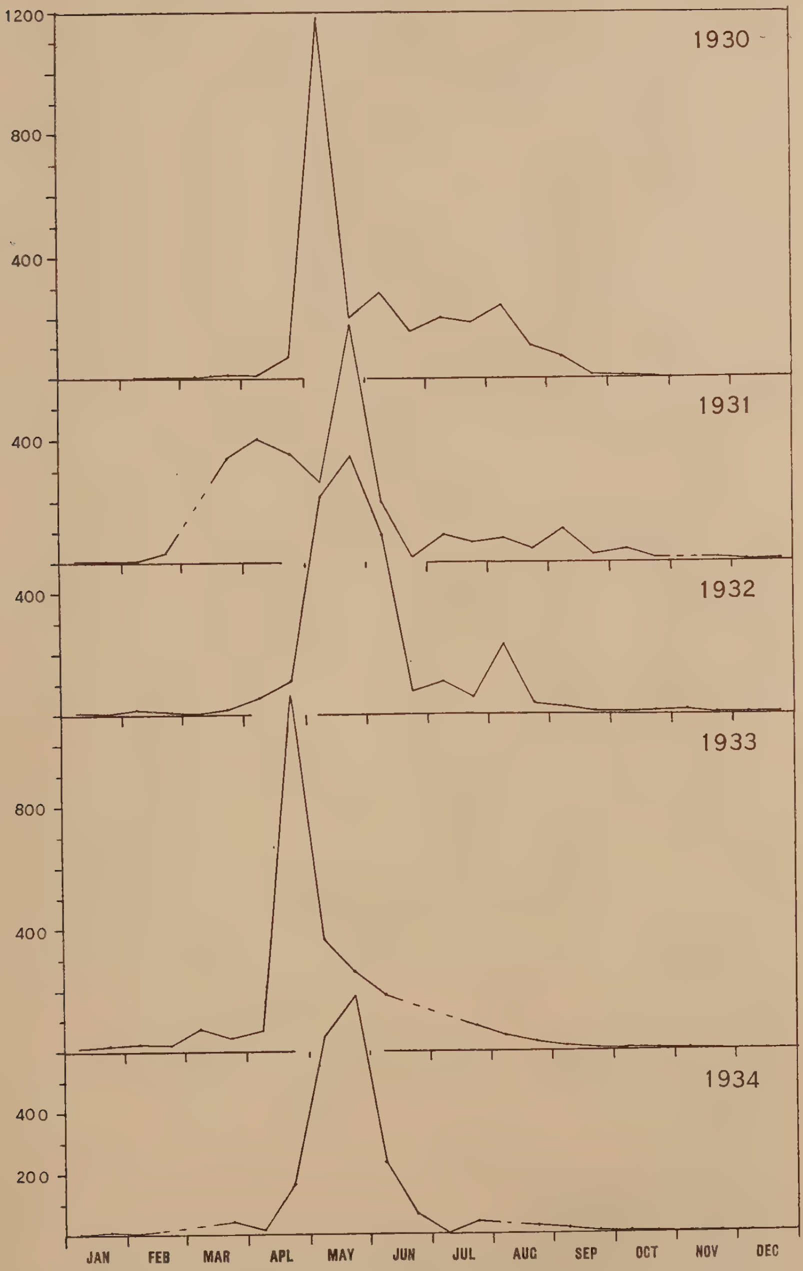

FIG. 3.—Curves showing the average catches in half-hour oblique hauls with the 2-metre ring-trawl for each fortnight for all young fish, excluding Clupeids, for each of the years 1930 to 1934 inclusive.

Comparison of Years 1930 to 1934.

The curves for the average fortnightly catches of all young fish (excluding clupeids) have been drawn for each of the years 1930 to 1934 in Figure 3. If these five years be compared it will be seen that while in 1930, 1932 and 1934 the post-larvæ of spring spawners begin to become abundant at about the same time, they appeared comparatively earlier in 1931 and 1933. These differences between the years are worth analysing further, and in Figures 4, 5, and 6 diagrams are given showing the actual catches on each day of collection in April, May, and June for the following six species: *G. merlangus*, *S. norvegicus*, *P. limanda*, *P. microcephalus*, *S. variegata*, and *C. lyra*. All these species show the same trend of alternating late and early years, though the actual times of abundance differ slightly for each species. When the curves are compared it is seen that there is a tendency for the species to fall into three groups: (1) *G. merlangus* and *P. limanda*, (2) *C. lyra* and *S. variegata*, and (3) *P. microcephalus* and *S. norvegicus*.

Let us examine first the most important of the non-Clupeid teleostean food-fishes in this area, the whiting, *G. merlangus*. In 1930 the time of maximum abundance was in the middle of May; in 1931 they already became abundant in the middle of April and after a falling off in numbers a renewed period of abundance extended to the third week in May; in 1932 the period of maximum abundance occurred in the last fortnight of May; in 1933 in the third week in April, and in 1934 in the first week in May. There may thus be a difference of as much as one month between the period of maximum abundance in one year and that in another.

If these differences in periods of abundance represent differences in the spawning times of the adult fish the majority of the young whiting occurring at the periods of maximum abundance should be approximately the same age. Otherwise an early peak might be composed of fish of a small size and a late peak of larger fish. Accordingly a number of fish were measured from catches made on the days on which the maximum catches occurred in each year. The results of measurement were as follows:—

	Length in millimetres.									
	4	5	6	7	8	9	10	11	12	13
May 15, 1930	—	—	14	9	4	2	2	—	—	—
May 25, 1932	—	4	33	31	11	9	5	—	—	—
April 21, 1933	—	11	28	25	28	9	6	2	—	—
May 2, 1934	1	8	12	20	15	6	—	1	2	—
April 16, 1931	7	24	20	12	8	5	5	2	—	—
May 21, 1931	—	—	7	6	14	10	3	7	3	7*

* A number caught above this size on this date have been omitted as being in association with Cyanea.

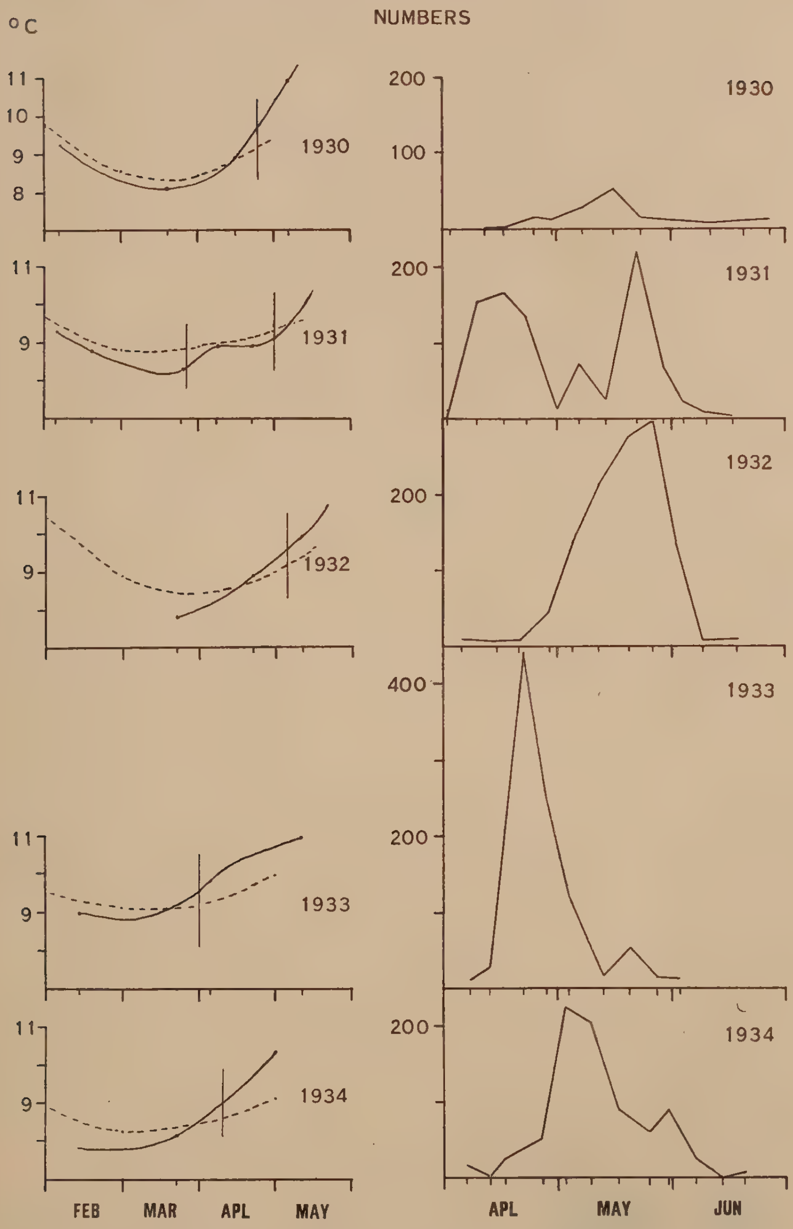

Fig. 4.—*Right:* Curves showing the actual catches of young whiting, *G. merlangus*, in half-hour oblique hauls with the 2-metre ring-trawl on each day of collection in the months April, May, and June for the years 1930 to 1934 inclusive.
Left: Temperatures in February, March, April and May for the years 1930 to 1934 inclusive. ———— surface at L5 : - - - - - bottom at E1.

From these figures it can be seen that the majority of the young whiting are on the average about 6 to 8 mm. in length at the periods of their maximum abundance in these collections. The year 1931, in which there were two peaks, has proved to be an exception in that the first peak consisted of younger and the second peak of older fish than on the average for the single peaks in the other four years.

In Figure 4, besides the curves for the abundance of young whiting, curves are given showing the temperatures of the water during the months February to May for each year. The data given are those for the surface water at L5 near the Eddystone and for the bottom water at E1 ten miles beyond. The L5 temperatures are taken from the Rapport Atlantique and data not yet published, and the E1 temperatures represent the temperatures at the beginning of each month read off from the smoothed curve and kindly supplied me by Mr. H. W. Harvey. Seeing that for the first three of these months the water is almost homogeneous from top to bottom in this area it is likely that these figures can be regarded as a very true picture of the temperature conditions. As is to be expected there is a tendency for the surface water at L5 to show a slightly greater extreme variation than the deeper offshore waters at E1.

Now Dannevig (1895, p. 149) found that the period required for the development of whiting eggs up to the point of hatching was 10¼ days at 8° C. and 8 days at 10° C. Heincke and Ehrenbaum (1900, p. 253) calculated it as 13·4 days at 8·7° C. We can assume therefore that the fish take about 10 days for their development in this region where the temperature drops to between 8° and 9° C. We do not know the rate of growth of the post-larvæ, but supposing that the majority of the post-larvæ during the peak periods were about 11 days old, this would mean that a period of three weeks had elapsed since the time of spawning. This figure is purely hypothetical, but is not likely to be very far wrong. If now we measure back a period of three weeks from the dates of maximum catches of young whiting on the curves in Figure 4 we can indicate the position of the hypothetical period of most intense spawning. These positions have been inserted as upright lines on the temperature curves in Figure 4. It is found that these lines nearly always coincide with temperatures somewhere between 9° and 9·5° C. In other words, the earliness or lateness of the peaks of maximum abundance of the post-larvæ corresponds with the times at which the temperatures are rising past 9° C. Whether we are right in assuming that this is the temperature at which most spawning occurs, or whether it may not rather be that we have under-estimated the age of the whiting and this temperature is that which stimulates a cessation of spawning, it is evident that there is a very close correlation between the temperature conditions and the period

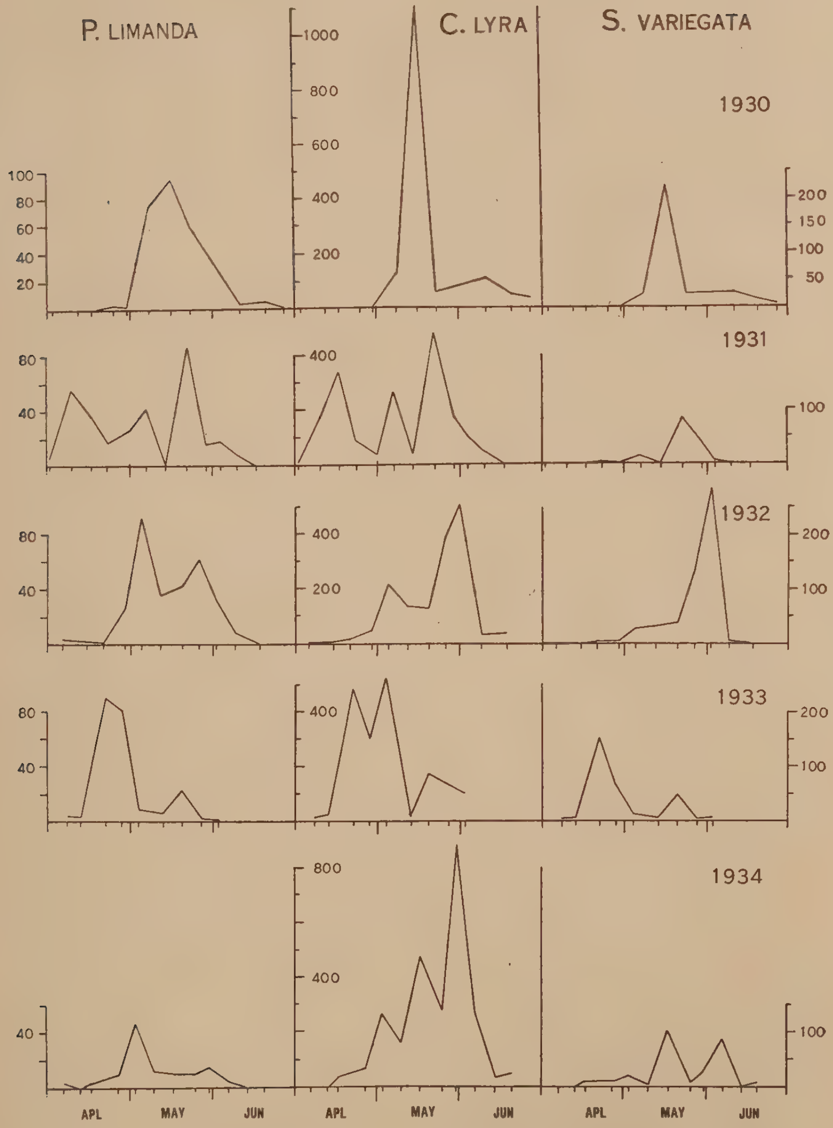

FIG. 5.—Curves showing the actual catches, in half-hour oblique hauls with the 2-metre ring-trawl, of post-larval *Pleuronectes limanda*, *Callionymus lyra*, and *Solea variegata* on each day of collection in the months April, May, and June for the years 1930 to 1934 inclusive.

of maximum abundance of the young fish. This receives further confirmation from a study of the conditions in 1931. In that year there were two peaks of abundance, and although the measurements showed that they consisted of younger and older fish respectively than did the peaks in other years, it would appear that spawning was somewhat irregular and prolonged. Inspection of the temperature conditions shows that a curious state of affairs existed in April when the temperature remained stationary at about 9° C. for two or three weeks. The upright lines coincide very nearly with this period and would do even more so were we to make allowance for the younger composition of the population at the first peak of abundance. Schmidt (1909) in his classical work on the pelagic fry of the gadoids gives the minimum temperature for spawning as *ca.* 5°–6° C. and the maximum as *ca.* 10° C. Damas (1909) also gives for the North Sea that the period of maximum spawning lies during April and May at temperatures between 6° and 10° C. Off Plymouth the temperature rarely drops below 8° C. and in some years does not drop below 9° C., so that evidently the period available for spawning is much more restricted than in more northern regions. This fact, coupled with the above evidence that the spawning period may be advanced or retarded by as much as a month, should be a matter of considerable importance in governing the success or otherwise of each year-class. It might well be that if hatching took place much before April the post-larvæ would be requiring an abundant food supply before the spring increase in the number of small copepods takes place. Also, as is shown below on page 167, the presence of other predatory planktonic organisms in large numbers at the same time as the period of maximum abundance of post-larvæ might effectively wipe out the young of one year-class since the short spawning period would not allow the production of a further supply of fry after the predatory animals had died down in numbers.

Examination of Figures 5 and 6 shows that the five species there given show essentially a similar story to that of the young whiting. There are slight differences, but no doubt these may be correlated with the fact that the temperature optimum for spawning varies slightly with the different species.

On the Changes in Abundance from Year to Year.

Many years have passed since the reality of large fluctuations in fish populations due to the production of good year-classes was first so ably shown by Hjort and his colleagues. Yet we are still without any direct evidence as to the causes of a good survival year or the failure of a brood. As possible factors which might determine the numerical value of a new year-class Hjort drew attention to the following two :—

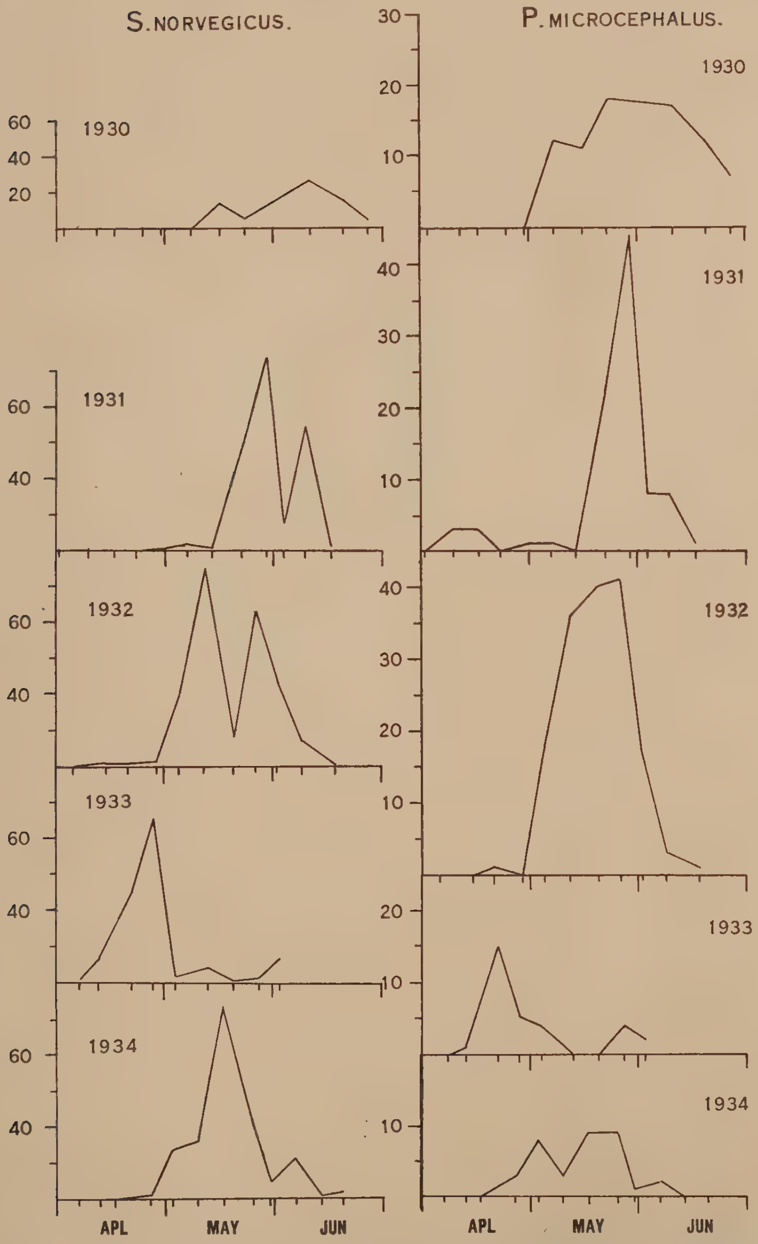

FIG. 6.—Curves showing the actual catches, in half-hour oblique hauls with the 2-metre ring-trawl, of post-larval *Scophthalmus norvegicus*, and *Pleuronectes microcephalus* on each day of collection in the months April, May, and June for the years 1930 to 1934 inclusive.

1. " That those individuals which at the very moment of their being hatched did not succeed in finding the very special food they wanted would die from hunger. That in other words the origin of a rich year-class would require the contemporary hatching of the eggs and the development of the special sort of plants or nauplii which the newly hatched larva needed for its nourishment."

2. " That the young larvæ might be carried far away out over the great depths of the Norwegian Sea, where they would not be able to return and reach the bottom on the Continental shelf before the plankton in the waters died out during the autumn months of the first year of their life. (Hjort, 1926, p. 33.)

Since then other possible causes have been suggested. Einar Lea (1930, p. 100) has shown that the success of hatching of herring may depend upon the thickness of the layer of their eggs on the bottom. He had noticed during hatching experiments that the eggs in the superficial layers developed living fry while those in the deeper layers failed to hatch. On examination for this phenomenon in nature he found that in the thick flakes of eggs deposited on the bottom while nearly all eggs had been fertilised and " had commenced hatching, only the embryos in the uppermost eggs were alive and could be brought to liberate themselves. The eggs in the deeper layers, necessarily deposited earlier than the eggs in the superficial layers, contained embryos at very different stages of development, while the bottom layers were found in a state of putrefaction."

Rollefsen (1930) has shown that only slight shaking is sufficient to produce abnormal development in healthy eggs of the cod. Consequent upon the discovery in nature of large numbers of eggs with deformed embryos in the plankton he has suggested that as the cod eggs float very near the surface the breakers in heavy seas may cause considerable mortality at this early stage in the cod's development and indeed in other fish whose eggs do not have a large perivitelline space.

Heavy gales may cause damage in other ways. For instance, in January, 1933, we experienced exceptionally heavy south-westerly gales which so disturbed the bottom as apparently to dislodge great numbers of adult Gebia from their burrows (Cooper, 1933 p. 61). The sea was so churned up that it was almost milky in colour. Such exceptional seas driving on to the shores along which many of our herring spawn might cause heavy damage among the newly hatched larvæ.

A direct correlation between the rich year-classes of the Norwegian cod and the years of smallest rainfall has been shown by Sund (1924), which shows that other meterological factors must also be kept in consideration as being ultimate factors bringing about the necessary conditions in the sea for the survival of a fish brood.

In watching for fluctuations in the abundance of fish fry it is necessary to know what magnitude of fluctuations we are to expect. Data for such a knowledge are scanty. Thompson (1930, p. 38) says of the North Sea haddock, "In the North Sea in the recent years prior to 1928 the most numerous brood was that of 1923. Reckoned on the basis of yield in unit of fishing time this brood outnumbered that of 1922 by more than 50 to one. The other year-classes gave yields placing them at various points between these extremes of success and non-success."

Poulsen (1930, p. 26) studying the fluctuations of the abundance of cod fry in the Kattegat and Belt Sea showed in a period of six years extreme differences of as much as 77 and 31 times between abundant and poor years. He traced these fluctuations in the abundance of the different year-classes among the adult fish. Johansen (1930, p. 82), on the basis of half-hour hauls with the 2-metre ring-trawl, found that the number of post-larval herring rose from an average of 6 in 1925 to 161 in 1928 in the Sound, and similarly from 16 to 160 in the Sound and adjacent parts of the Baltic. This increase was paralleled by a similar increase in the yield of the herring fisheries. He also showed a similar correspondence between the number of fry and adults of the haddock in the Belt Sea in 1925–26 (1926). These latter two examples cannot however be regarded so much as effects of survival as of actual incursions of large numbers of spawning fish into the areas in question.

With such degrees of fluctuation in mind then let us examine the results of the young fish collections off Plymouth. Taking the years 1930 to 1934 I have given below figures showing the sum of the average monthly catches for the whole period (last column but one in Table I) divided by the corresponding figures for the best and worst years (last column in Table IV) for a number of species of fish. A column is also inserted giving the results of dividing the yearly averages of the best year by those of the worst year for the same species of fish. I have included here only those species whose yearly average shown in Table I exceeds 20 in number.

	Best/Av. year/1930–34.	Worst/Av. year/1930–34.	Best/ /Worst.	1929/Av. /1930–34.
G. merlangus	1·6 (1932)	0·3 (1930)	6·2	0·50
G. minutus	3·0 (1931)*	0·4 (1933)	8·3	0·14
Onos spp.	2·3 (1930)	0·4 (1932)	5·3	0·13
Arnoglossus spp.	2·1 (1931)	0·2 (1934)	11·5	1·30
S. norvegicus	1·5 (1932)	0·4 (1930)	3·7	0·36
P. limanda	1·5 (1931)	0·5 (1934)	3·4	0·76
P. microcephalus	1·8 (1932)	0·4 (1934)	5·1	0·18
S. variegata	1·6 (1932)	0·4 (1931)	3·6	0·09
Callionymus spp.	1·1 (1930)	0·9 (1932)	1·2	0·46
S. scombrus	2·6 (1930)	0·5 (1933)	5·1	2·68
Gobiid spp.	2·8 (1930)	0·2 (1933)	11·9	2·08

* This year has weighted the average for 1930–34.

These figures show that in none of the years 1930 to 1934 did the best years exceed the average by more than three times, and the worst year with two exceptions (Arnoglossus spp. and Gobiid spp.) was never less than a quarter of the average. The third column shows that with only four exceptions the best years never exceeded the worst by more than five times. The exceptions were Gobiid spp. and Arnoglossus spp. which are summer spawners and are discussed below (p. 169); *G. minutus* with a maximum difference of eight times and *G. merlangus* with a difference of only six times, neither of which greatly exceed the figures for other species. In these figures there is also no indication of any marked relation between the best and worst years. In the previous report (Russell, 1930, b, p. 710) it was remarked that there was "an indication that the post-larval stages of certain spring spawners were but poorly represented in the year 1929." Accordingly I have given above with the results for 1930 to 1934 a column showing the relation between the 1929 catches and the average for 1930 to 1934. It shows that with three exceptions the 1929 catches fell below the average. The exceptions were Arnoglossus spp., *S. scombrus*, and Gobiid spp., all of which are summer spawners. It is evident therefore that conditions in 1929 had affected adversely all the remaining fish, all of which are spring spawners having their maximum abundance of post-larvæ in the months of April or May. These results are worth examining in more detail, and accordingly in Figure 7 have been plotted the total catches of young fish on each day of collection in 1929. When this figure is compared with Figure 3 the abnormal form of the curve is at once evident. The large spring peak that fell in April or May in other years is absent. There is a peak on one day in July that has been produced by young mackerel and gobies and

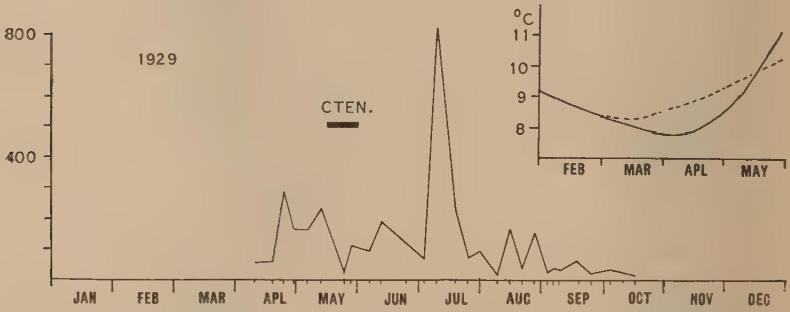

FIG. 7.—Curve showing the actual catches of all young fish, excluding Clupeids, in half-hour oblique hauls with the 2-metre ring-trawl on each day of collection in the year 1929. The temperatures for the months February to May are also given for the same year. ———— surface at L5; – – – – – bottom at E1. CTEN: Period during which Ctenophores were abundant.

these are summer spawners. In other words, the peak usually produced by the spring spawners is absent.

In Figure 7 has also been inserted a curve showing the temperature conditions in the early months of the year. If this be compared with the temperature curves given in Figure 4 it can be seen that 1929 was a late year, comparable to 1932 when a temperature of 9° C. was only reached between the end of April and beginning of May. This being so we should have expected the spring peak in abundance to have occurred in 1929 as in 1932 towards the last week in May.

It is worthy of mention that I made the following notes when making the young fish records.

May 15th, 1929.	" Much ctenophore."
May 23rd, 1929.	" Masses of ctenophores."
May 27th, 1929.	" Much ctenophore."
June 6th, 1929.	" Ctenophores almost entirely gone."

In the same year Berrill (1930, p. 753) notes a profusion of the siphonophore *Stephanomia bijuga* in Salcombe estuary on May 17th–19th coinciding " with a similar abundance of the three Ctenophores commonly occurring in these waters, namely *Beroe cucumis* Fabricius, *Bolina infundibulum* Fabricius and *Pleurobrachea pileus* Fabricius, and not only were these abundant, but they also had reached what is possibly their maximum size. Individuals of Beroe frequently were seen of at least six inches in length. Ten days later all trace of Siphonophores and Ctenophores had vanished, with the exception of some small individuals of Beroe, and these last were not seen to approach the large size already mentioned until after two months." Since that year all Ctenophores have been counted in the ring-trawl collections, and it has been found that it is usual for there to be an increase in abundance at this time of year. From the above notes it is evident, however, that in May, 1929, they must have been exceptionally abundant, and one cannot escape the possible conclusion that they may have been responsible for the absence of the peak in the abundance of young fish which should have occurred just at the same time. The voracity of Ctenophores is well known. Bigelow (1926, p. 368) has remarked that the smaller plankton animals " are locally exterminated in the centres of abundance for Pleurobrachia " and that it is common to find them packed with copepods or euphausiids, and larval fishes.

Whether this supposition be correct or not, it is at any rate certain that in May, 1929, there was some factor that affected the abundance of post-larvæ of all species of spring spawning fish indiscriminately.

During the eleven years period of observations there have only been two instances of excessive fluctuations in numbers of post-larvæ. In 1926 young mackerel were unusually abundant (see the 1930 report, p. 710). In that year the sum of the average monthly catches was nearly sixteen times greater than the average for the 1930–34 period. In the winter of 1932 herring larvæ were unusually abundant, the yearly average being 152 as against the next highest of 9 in 1933. Young sprat were also very abundant in March, 1931, but these were mostly newly hatched specimens.

On the Change in Abundance of Post-larval Whiting.

Although we have found no evidence of any considerable fluctuation in the abundance of post-larval whiting there are indications that a change has taken place in their numbers to a small extent during the eleven years of observation. A comparison of the results for 1930 to 1934 with those for 1924 to 1929 given in the previous report shows that on the average young whiting have been more abundant during the later period, the sum of the average monthly catches being 196 as opposed to 131 for the earlier period. Closer examination shows that the year 1930 was the culminating year of the period of low production which started in 1925 and possibly in 1924 (in which year only two samples were obtained in May and June). The sums of the average monthly catches for each year 1925 to 1934 (1928 excluded) have been plotted in the form of a graph in Figure 8. The greater abundance of young whiting in the later years is obvious.

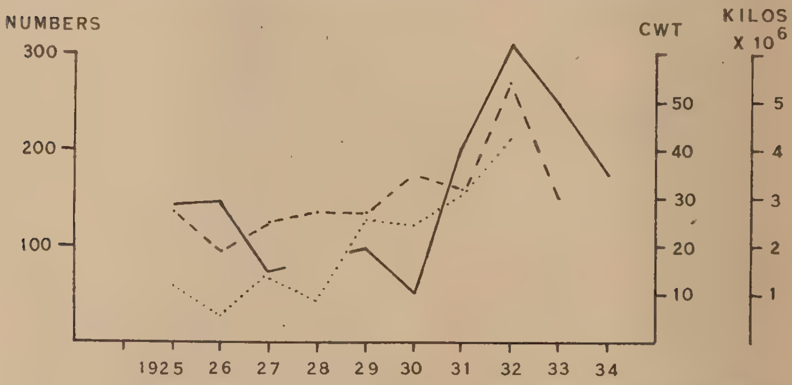

Fig. 8.—Curves showing the sums of the average monthly catches of young whiting, *G. merlangus*, in half-hour oblique hauls with the 2-metre ring-trawl, for each year 1925 to 1934 (except 1928) (————); the landings of whiting in cwt. per 100 hours' fishing in the English Channel, area VII d–e, by British sailing trawlers (– – – – –); and the total landings of whiting by French boats in the western end of the English Channel, area VII e (. . . . .).

It is unlikely that this change in abundance is due to a shift in the spawning area. The whiting is known to spawn over a large area in the southern North Sea and Schmidt's results (1909) indicate that the post-larvæ are similarly distributed all over the English Channel.

Examination of the statistics of landings for the English Channel shows that there has apparently been a similar increase in the numbers of adult fish. In Figure 8 have also been plotted the yearly landings of whiting in cwt. per 100 hours' fishing in the English Channel (Area VII d–e) by British sailing trawlers. It is rather remarkable that this curve shows the same trend as that of the curve for abundance of the post-larvæ. In the same figure are also plotted the landings of whiting by French boats from the western English Channel (Area VII e), in this case given only as total weights landed. The same trend is again shown. In this comparison the agreement in all three curves in the peak year 1932 is striking. There thus seems to be some evidence that we are witnessing a slow change in the abundance of whiting in the English Channel, and that the increase in the number of post-larvæ is due rather to an increase in the numbers of spawning fish caused possibly by a gradual improvement in survival, than to the great success of any one year. It must be admitted that the evidence is slender, but it is at any rate sufficiently noticeable to be worthy of mention.

It is also possibly not without significance that over the same period the abundance of Callionymus post-larvæ has decreased, the sum of the monthly averages having fallen from 965 for the period 1924–29 to 547 for the period 1930–34. Next to Callionymus the whiting is the most abundant species in our spring collections, and the destruction of large numbers of the former by fine meshed trawls might produce a beneficial effect on the stock of other fish. Again the evidence is slender but is worth future attention. The abundance of Callionymus during the period 1930–34 has shown remarkable constancy, the best and worst years showing yearly averages of 500 and 582.

On the Decrease in Abundance of Summer Spawners.

While this gradual change in the abundance of young of the above species of spring spawning fish is to be noticed, a change in the abundance of those of summer spawning fish also seems to have taken place. Examination of the curves for the fortnightly averages of total young fish for each year in Figure 3 (p. 157) shows that there has been a progressive decrease in the number of post-larvæ that occur during the months July and August. Figures are given below for the sum of the monthly average catches in each year for those species of fish whose post-larvæ show maximal abundance in the months June, July, August, September and October (see Table II), excluding Clupeids.

1930	403
1931	230
1932	197
1933	117
1934	79

The significance of this decline in numbers is not obvious. It will be necessary to follow it up with further observations when perhaps it may be found possible to link it up with other changes that have taken place in the plankton in this area.

There is, however, one indication worthy of mention. We have already drawn attention on page 150 and Figure 2 to the greater numbers of young of summer spawners during the period 1924–29 than during the period 1930–34. Now it is natural to suppose that the potential productivity of any given water mass depends upon the amount of nutrient salts available in the water. Starting with a considerable amount of nutrient salt accumulated during the winter months we have in this area a sequence of events characterised by a heavy spring production of plankton when a large proportion of the nutrient matter available is used up, and this increase is followed by successive smaller increases during the summer months utilising the nutrient material left over after the spring increase and that which is becoming once more available due to the death of organisms earlier in the year. If by any chance the available nutrient matter at the beginning of the year should be less than usual we should expect it to show its effects on the plankton production during the summer months, since a greater proportion than usual will have been utilised by the spring increase. It is interesting to find that we can trace a possible connexion between the abundance of young of the summer spawning fish and the amount of phosphate available at the beginning of the year.

I am indebted to Dr. L. H. N. Cooper for the following figures for the maximum amount of phosphorus found in the water for the winter months in each year during the period of our observations, calculated from his own analyses and those of Dr. W. R. G. Atkins published in this Journal.

WINTER MAXIMA FOR PHOSPHATE AT E1.

Mean content of water column as mg. P per cubic metre corrected for salt error.

Year.	Maximum.	Date.	% deviation from mean.
1923–24	20·5	Jan. 2	+19
1924–25	17·5	Dec. 9	nil.
1925–26	22	Jan. 12	+27
1926–27	16·5	Dec. 13	— 5
1927–28	19	Jan. 31	+10
1928–29	17	Jan. 2	nil.
1929–30	—	—	—
1930–31	16	Dec. 4	— 7
1931–32	13·5	Jan. 28*	—22
1932–33	15·5	Jan. 11	—10
1933–34	14	Dec. 15	—19
Mean	17·25		

The latter period of observations here stands out as a period of low phosphate content and it is the period during which the numbers of young fish were low during the summer months.

If we analyse the results for the period 1924–29 further, we obtain the following figures for summer-spawning fish (excluding Clupeids) in comparison with those given above for 1930–34.

1924	696
1925	140
1926	909
1927	170
1928	(no records)
1929	321

Is it significant that the two outstanding years, 1924 and 1926, were years in which the initial phosphorus content of the water was high ? These two years also stand out in my memory as being years when the macroplankton in the ring-trawl collections was very abundant during the summer months and the Clupeids showed a similar abundance (see Russell, 1930, b. Table III). In these two years also it was noticeable that the post-larvæ of *Molva molva* were unusually abundant (see 1930 Report, p. 715). The ling is a fish which spawns over the deep waters of the Atlantic shelf and it is possible that here we have a clue to the origin of this phosphate-rich water which was evidently drawn from a different source from that in other years. It is hoped later to link these changes with the occurrence of other planktonic organisms (see Russell, 1935, p. 321).

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* No data after Jan. 28th.

SUMMARY.

Data are given on the abundance of post-larval stages of teleostean fish in half-hour oblique hauls with the 2-metre stramin ring-trawl taken at weekly intervals at a position two miles east of the Eddystone lighthouse during the years 1930 to 1934 inclusive.

The seasonal composition of the catches is considered and it is shown that there is a gradual change over from the young of northern species of fish to those of more southern species as the summer advances. The relation between the spawning times of closely related species appears usually to be a function of their geographic distribution.

The period of maximum abundance of post-larvæ of spring-spawning fish occurs at different times in different years and this difference may be as much as a month. An apparent correlation between the times of abundance of young whiting and the previous temperature of the water has been shown.

During the period 1924 to 1934 there have been no indications of very great fluctuations in the numbers of young fish except possibly once with the mackerel and once with the herring.

There are indications that the young of the whiting have increased slightly in abundance during the last five years, and a similar increase has been shown in the landings of whiting from the English Channel. The abundance of post-larval Callionymus has correspondingly decreased. There has also been a decrease in the numbers of young of summer-spawning species, and a possible connexion between their abundance and the amount of phosphate available in the water at the beginning of the year is shown.

In 1929 the normal peak of abundance of the young of spring-spawning fish was absent. There are indications that this may possibly have been caused by large numbers of Ctenophores present in the area at the time when the peak of abundance should have occurred.

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TABLE III.

Dates on which Collections were made.

Year.	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.
1930		4 12 19 26	5 12 19 27	2 11 16 24 29	7 15 22	10 19 26	4 9 14 23 29	7 14 21 28	3 11 16 24	1 7 14 16	6 13 20 26	3 10 17 22
1931	1 5 15 22 26	6 12 20 23	17 26	1 9 16 22 30	6 13 21 28	3 9 16	8 15 23 30	5 14 21 28	3 10 17 24	1 8 15 22 29	25	4 9 16 22 30
1932	7 12 19 26	3 10 17	9 16 23 30	5 14 20 28	4 11 19 25	1 8 17	5 14 21 27	5 10 17 26	1 7 14 21 29	4 11 19 26	14 22	1 7 13 21
1933	4 12 18 27	2 8 17	8 15 23† 30	7 12 21 27	3 12 19 26	2	19 27	2 10 16 23 30	7 15 21 28	5 12 18 25	15 23 29	6 12 19 28
1934	3 10 19 24 31	7 15	16 23 29	6* 12 16 26	2 9 16 24 29	6 13 19	10 17 22 30	16 22 31	6 13 21 26	3 11 18‡ 24 31	7 15	3 11 19§ 29

* Revelstoke 4 mi. N. † L4–L5. ‡ L6. § L3.

TABLE IV.

AVERAGE MONTHLY CATCHES OF POST-LARVÆ PER HALF-HOUR OBLIQUE HAUL WITH 2-METRE RING-TRAWL.

	Year.	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total Young Fish	1930		21	52	74	897	246	237	261	52	4	–	1	1845
	1931	28	312	2423	612	563	168	96	74	67	43	32	10	4428
	1932	162	405	193	136	901	446	96	142	38	99	46	4	2668
	1933	25	438	122	660	321	216	103	37	44	169	12	–	2147
	1934	95	16	121	164	796	219	49	45	14	80	17	13	1629
Ditto, less Clupeids	1930		3	7	43	854	198	194	175	41	2	–	–	1517
	1931	2	16	340	376	521	136	75	60	65	19	11	4	1625
	1932	3	14	11	81	781	420	83	134	17	5	6	1	1556
	1933	12	21	57	618	313	185	80	36	9	4	2	–	1337
	1934	7	4	40	93	728	179	32	30	12	7	10	2	1144
All Clupeids spp. Herring, Sprat, Pilchard	1930		18	45	31	43	48	43	86	11	2	–	1	328
	1931	26	296	2083	236	42	32	21	14	2	24	21	6	2803
	1932	159	391	182	54	120	26	13	8	21	94	40	3	1111
	1933	13	417	65	42	8	31	23	1	35	165	10	–	810
	1934	88	12	81	71	68	40	17	15	2	73	7	11	485
Clupea harengus (with yolk-sac) Herring	1930		7	+	–	–	–	–	–	–	–	–	–	7
	1931	4	–	–	–	–	–	–	–	–	–	–	1	5
	1932	138	–	14	–	–	–	–	–	–	–	–	–	152
	1933	–	8	1	–	–	–	–	–	–	–	–	–	9
	1934	–	–	2	–	–	–	–	–	–	–	–	–	2
Gadus pollachius Pollach	1930		–	–	3	24	–	–	–	–	–	–	–	27
	1931	–	–	1	+	7	1	–	–	–	–	–	–	9
	1932	–	–	–	4	16	1	–	–	–	–	–	–	21
	1933	–	–	1	3	–	–	–	–	–	–	–	–	4
	1934	–	–	–	2	3	–	–	–	–	–	–	–	5
Gadus merlangus Whiting	1930		–	–	6	32	9	3	–	–	–	–	–	50
	1931	–	–	–	94	97	11	2	–	–	–	–	–	204
	1932	–	–	3	18	233	52	+	2	–	–	–	–	308
	1933	–	+	2	183	51	11	1	–	–	–	–	–	248
	1934	–	–	5	25	134	11	+	–	–	–	–	–	175
Gadus minutus Poor Cod or Bib	1930		–	–	19	37	+	–	–	–	–	–	–	56
	1931	–	9	175	80	18	–	–	–	–	–	–	–	282
	1932	–	–	1	10	52	1	–	–	–	–	–	–	64
	1933	–	–	21	12	1	–	–	–	–	–	–	–	34
	1934	–	–	2	17	19	–	–	–	–	–	–	–	38
Gadus luscus Pouting or Pout	1930		–	–	1	7	1	–	1	–	1	–	–	11
	1931	1	1	7	4	3	–	–	+	+	4	10	5	35
	1932	3	8	1	1	4	+	–	1	+	1	5	1	25
	1933	7	3	1	3	+	–	1	1	+	2	2	–	20
	1934	4	1	2	1	1	–	–	1	+	+	2	1	13
Gadus callarius Cod	1930		–	–	+	–	–	–	–	–	–	–	–	+
	1931	–	+	–	–	–	–	–	–	–	–	–	–	+
	1932	–	–	–	–	–	–	–	–	–	–	–	–	–
	1933	–	–	+	–	–	–	–	–	–	–	–	–	+
	1934	–	–	+	–	–	–	–	–	–	–	–	–	+
Onos sp. Rockling	1930		–	–	4	105	8	+	–	–	–	–	–	117
	1931	–	–	3	13	8	8	–	–	–	–	–	–	32
	1932	–	–	+	7	13	2	+	–	–	–	–	–	22
	1933	–	–	4	47	1	4	1	–	–	–	–	–	57
	1934	–	–	–	9	21	3	+	–	–	+	1	–	34
Molva molva Ling	1930		–	–	–	1	+	–	–	–	–	–	–	1
	1931	–	–	–	–	1	+	–	–	–	–	–	–	1
	1932	–	–	–	–	3	2	–	–	–	–	–	–	5
	1933	–	–	–	–	+	1	–	–	–	–	–	–	1
	1934	–	–	–	–	1	–	–	–	–	–	–	–	1
Merluccius merluccius Hake	1930		–	–	–	–	+	–	+	–	–	–	–	+
	1931	–	–	–	–	–	–	–	–	+	–	–	+	+
	1932	–	–	–	–	–	–	–	+	–	+	–	–	+
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–

	Year.	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Raniceps raninus Lesser Forkbeard	1930		–	–	–	–	–	+	1	–	–	–	–	1
	1931	–	–	–	–	–	–	–	–	–	–	–	–	–
	1932	–	–	–	–	–	–	–	–	–	–	–	–	–
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	–	–	–	–	+	–	–	+
Capros aper Boar-fish	1930		–	–	–	–	–	1	1	+	–	–	–	2
	1931	–	–	–	–	–	–	–	1	–	–	–	–	1
	1932	–	–	–	–	–	–	–	–	+	–	–	–	+
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Zeus faber John Dory	1930		–	–	–	–	–	–	–	+	–	–	–	+
	1931	–	–	–	–	–	–	–	–	–	–	–	–	–
	1932	–	–	–	–	–	–	–	+	–	–	–	–	+
	1933	–	–	–	–	–	–	–	1	+	+	–	–	1
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Arnoglossus sp. Scaldbacks	1930		–	–	–	–	3	10	27	26	+	–	–	66
	1931	–	–	–	–	–	+	6	11	47	5	–	–	69
	1932	–	–	–	–	–	–	2	5	7	1	–	–	15
	1933	–	–	–	–	–	–	2	6	3	1	–	–	12
	1934	–	–	–	–	–	+	2	2	1	+	1	–	6
Rhombus lævis Brill	1930		–	–	–	1	–	–	–	–	–	–	–	1
	1931	–	–	–	+	+	–	–	–	–	–	–	–	+
	1932	–	–	–	–	–	–	+	–	+	–	–	–	+
	1933	–	–	–	–	–	–	+	+	–	–	–	–	+
	1934	–	–	–	–	+	+	–	–	–	–	–	–	+
Rhombus maximus Turbot	1930		–	–	–	–	+	+	–	1	–	–	–	1
	1931	–	–	–	–	–	+	1	–	–	–	–	–	1
	1932	–	–	–	–	–	–	+	1	–	–	–	–	1
	1933	–	–	–	–	–	–	1	2	+	–	–	–	3
	1934	–	–	–	–	–	–	+	1	–	–	–	–	1
Scophthalmus norvegicus Norway Topknot	1930		–	–	–	6	15	2	–	–	–	–	–	23
	1931	–	–	–	+	42	29	2	+	–	–	–	–	73
	1932	–	–	–	1	63	21	+	1	–	–	–	–	86
	1933	–	–	1	39	4	13	2	–	–	–	–	–	60
	1934	–	–	–	1	43	9	1	–	–	–	–	–	54
Zeugopterus punctatus Topknot	1930		–	–	–	2	–	–	–	–	–	–	–	2
	1931	–	–	–	+	4	1	–	–	–	–	–	–	5
	1932	–	–	–	+	7	4	–	–	–	–	–	–	11
	1933	–	–	–	7	–	–	–	–	–	–	–	–	7
	1934	–	–	–	1	2	+	–	–	–	–	–	–	3
Pleuronectes limanda Dab	1930		–	–	1	76	3	–	–	–	–	–	–	80
	1931	–	–	12	28	36	8	–	–	–	–	–	–	84
	1932	–	–	1	8	58	13	–	–	–	–	–	–	80
	1933	–	–	1	45	10	1	–	–	–	–	–	–	57
	1934	–	–	2	4	18	1	–	–	–	–	–	–	25
Pleuronectes flesus Flounder	1930		–	–	1	–	–	–	–	–	–	–	–	1
	1931	–	–	2	4	1	–	–	–	–	–	–	–	7
	1932	–	–	–	2	10	1	–	–	–	–	–	–	13
	1933	–	–	1	1	1	–	–	–	–	–	–	–	3
	1934	–	–	–	+	–	–	–	–	–	–	–	–	+
Pleuronectes microcephalus Merrysole or Lemon Dab	1930		–	–	+	14	12	1	–	–	–	–	–	27
	1931	–	–	3	1	17	6	+	–	–	–	–	–	27
	1932	–	–	–	+	34	7	–	–	–	–	–	–	41
	1933	–	–	–	5	2	2	–	–	–	–	–	–	9
	1934	–	–	–	1	6	1	–	–	–	–	–	–	8
Solea vulgaris Common Sole	1930		–	–	2	7	–	–	–	–	–	–	–	9
	1931	–	–	3	6	2	–	–	–	–	–	–	–	11
	1932	–	–	+	2	2	1	–	–	–	–	–	–	5
	1933	–	–	–	1	1	–	–	–	–	–	–	–	2
	1934	–	–	+	1	+	–	–	–	–	–	–	–	1
Solea variegata Thickback	1930		–	–	–	90	13	3	1	–	–	–	–	107
	1931	–	–	–	+	33	1	1	1	–	–	–	–	36
	1932	–	–	–	2	56	71	1	+	–	–	–	–	130
	1933	–	–	1	56	17	6	–	–	–	–	–	–	80
	1934	–	–	+	5	31	30	1	–	–	–	–	–	67
Solea lascaris Sand Sole	1930		–	–	–	–	–	–	–	+	+	–	–	+
	1931	–	–	–	–	–	–	–	–	–	–	–	–	–
	1932	–	–	–	–	–	–	–	+	+	–	–	–	+
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	–	+	–	–	–	–	–	+

	Year.	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Serranus cabrilla	1930		–	–	–	–	–	–	–	1	–	–	–	1
Sea Perch	1931	–	–	–	–	–	–	–	1	+	–	–	–	1
	1932	–	–	–	–	–	–	–	+	2	–	–	–	2
	1933	–	–	–	–	–	–	–	1	+	–	–	–	1
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Caranx trachurus	1930		–	–	–	–	–	1	17	7	+	–	–	35
Horse Mackerel or Scad	1931	–	–	–	–	–	–	1	4	6	+	–	–	11
	1932	–	–	–	–	–	–	+	6	1	–	–	–	7
	1933	–	–	–	–	–	–	3	8	1	–	–	–	12
	1934	–	–	–	–	–	–	1	3	9*	–	–	–	13
Mullus surmuletus	1930		–	–	–	–	–	+	–	–	–	–	–	+
Red Mullet	1931	–	–	–	–	–	–	–	–	–	–	–	–	–
	1932	–	–	–	–	–	–	–	+	–	–	–	–	+
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Morone labrax	1930		–	–	–	–	–	–	–	–	–	–	–	–
Bass	1931	–	–	1	+	+	–	–	–	–	–	–	–	1
	1932	–	–	–	–	–	–	–	–	–	–	–	–	–
	1933	–	–	–	+	–	–	–	–	–	–	–	–	+
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Ammodytes ? tobianus	1930		1	2	+	–	–	–	–	–	–	–	–	3
Lesser Sandeel	1931	1	1	58	5	1	+	1	–	+	1	–	+	68
	1932	1	5	3	1	–	–	–	–	+	–	–	–	10
	1933	5	12	18	1	–	–	–	+	–	+	–	–	36
	1934	–	–	15	1	–	–	+	+	–	1	–	–	17
Ammodytes lanceolatus	1930		–	2	–	1	2	3	14	+	–	–	–	22
Greater Sandeel	1931	–	–	–	–	9	4	4	2	1	–	–	–	20
	1932	–	–	–	8	13	6	2	4	+	+	–	–	33
	1933	–	–	–	11	1	5	2	+	–	–	–	–	19
	1934	2	2	–	+	23	1	1	2	–	1	–	–	32
Cepola rubescens	1930		–	–	–	–	–	–	+	–	–	–	–	+
Red Band Fish	1931	–	–	–	–	–	–	–	1	–	–	–	–	1
	1932	–	–	–	–	–	–	–	–	+	–	–	–	+
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Callionymus spp.	1930		–	–	2	431	65	59	23	2	–	–	–	582
Dragonets	1931	–	+	50	129	240	48	9	17	5	9	1	–	508
	1932	–	–	+	18	215	191	15	59	1	1	–	–	500
	1933	–	–	5	206	211	102	44	5	1	1	–	–	575
	1934	–	–	–	26	410	112	12	6	+	2	6	1	575
Labrus bergylta	1930		–	–	–	–	1	+	–	–	–	–	–	1
Ballan Wrasse	1931	–	–	–	–	1	2	–	–	–	–	–	–	3
	1932	–	–	–	–	+	4	2	–	–	–	–	–	6
	1933	–	–	–	–	–	5	–	–	–	–	–	–	5
	1934	–	–	–	–	2	–	–	–	–	–	–	–	2
Labrus mixtus	1930		–	–	–	–	2	–	–	–	–	–	–	2
Cuckoo Wrasse	1931	–	–	–	–	+	–	–	–	–	–	–	–	+
	1932	–	–	–	–	–	–	–	–	–	–	–	–	–
	1933	–	–	–	–	–	1	–	–	–	–	–	–	1
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Ctenolabrus rupestris	1930		–	–	–	–	2	27	15	1	–	–	–	45
	1931	–	–	–	–	–	–	7	1	–	–	–	–	8
	1932	–	–	–	–	–	–	10	2	+	–	–	–	12
	1933	–	–	–	–	–	1	1	–	–	–	–	–	2
	1934	–	–	–	–	–	–	1	+	–	–	–	–	1
Crenilabrus melops	1930		–	–	–	–	1	2	+	–	–	–	–	3
	1931	–	–	–	–	–	1	1	+	–	–	–	–	2
	1932	–	–	–	–	–	–	+	–	–	–	–	–	+
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	+	–	+	–	–	–	–	+
Centrolabrus exoletus	1930		–	–	–	–	–	2	+	–	–	–	–	2
	1931	–	–	–	–	–	–	1	–	–	–	–	–	1
	1932	–	–	–	–	–	–	3	1	–	–	–	–	4
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Trachinus vipera	1930		–	–	–	–	–	2	7	1	–	–	–	10
Lesser Weever	1931	–	–	–	–	–	–	4	4	–	–	–	–	8
	1932	–	–	–	–	–	–	2	4	+	–	–	–	6
	1933	–	–	–	–	–	–	4	2	1	–	–	–	7
	1934	–	–	–	–	–	–	1	2	–	–	–	–	3

* 80–90 mm. long.

	Year.	Jan.	Feb.	March.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Trachinus draco	1932	August 26th, 2												
Greater Weever														
Scomber scombrus	1930		–	–	–	–	40	12	3	1	–	–	–	56
Mackerel	1931	–	–	–	–	–	7	6	5	+	–	–	–	18
	1932	–	–	–	–	–	2	11	1	+	–	–	–	14
	1933	–	–	–	–	–	–	10	1	–	–	–	–	11
	1934	–	–	–	–	–	2	7	6	–	–	–	–	15
Gobius spp.	1930		2	–	–	+	16	51	49	1	+	–	–	119
Gobies	1931	–	–	1	+	1	5	19	4	1	1	1	–	33
	1932	–	–	–	–	1	6	5	39	+	–	–	–	51
	1933	+	–	+	–	8	–	1	1	+	–	–	–	10
	1934	–	–	–	–	7	5	1	2	–	–	1	+	16
Lebetus scorpioides	1930		–	–	–	–	–	+	1	+	–	–	–	1
	1931	–	–	–	–	–	+	+	+	1	+	–	–	1
	1932	–	–	–	–	–	–	1	2	1	+	–	–	4
	1933	–	–	–	–	–	–	1	2	1	–	+	–	4
	1934	–	–	–	–	–	–	–	1	+	+	–	–	1
Blennius pholis	1930		–	–	–	–	–	+	–	–	–	–	–	+
Shanny	1931	–	–	–	–	–	–	–	+	–	–	–	–	+
	1932	–	–	–	–	–	–	–	–	–	–	–	–	–
	1933	–	–	–	–	+	–	–	–	–	–	–	–	+
	1934	–	–	–	–	+	–	–	–	–	–	–	–	+
Blennius ocellaris	1930		–	–	–	–	–	–	1	+	–	–	–	1
Butterfly Blenny	1931	–	–	–	–	–	–	–	–	1	–	–	–	1
	1932	–	–	–	–	–	–	–	1	–	–	–	–	1
	1933	–	–	–	–	–	–	–	+	–	–	–	–	+
	1934	–	–	–	–	–	–	+	–	–	–	–	–	+
Blennius gattorugine	1930		–	–	–	–	+	4	7	+	–	–	–	11
Tompot	1931	–	–	–	–	–	–	9	2	+	–	–	–	11
	1932	–	–	–	–	+	–	26	3	+	–	–	–	29
	1933	–	–	–	–	–	–	4	3	–	–	–	–	7
	1934	–	–	–	–	–	–	2	1	–	–	–	–	3
Chirolophis galerita	1930		–	1	+	–	–	–	–	–	–	–	–	1
Yarrell's Blenny	1931	1	5	21	–	–	–	–	–	–	–	–	–	[illegible]7
	1932	–	1	2	–	–	–	–	–	–	–	–	–	3
	1933	–	4	1	–	–	–	–	–	–	–	–	–	5
	1934	–	1	1	–	–	–	–	–	–	–	–	–	2
Agonus cataphractus	1930		–	–	+	–	–	–	–	–	–	–	–	+
Pogge	1931	–	–	–	+	–	–	–	–	–	–	–	–	+
	1932	–	–	–	–	–	–	–	–	–	–	–	–	–
	1933	–	–	–	–	–	–	–	–	–	–	–	–	–
	1934	–	–	–	–	–	–	–	–	–	–	–	–	–
Trigla spp.	1930		–	–	+	13	3	4	6	1	–	–	–	27
Grey and Red	1931	–	–	–	3	3	1	2	5	3	–	–	–	17
Gurnards, and Tub	1932	–	–	–	–	2	6	1	2	1	+	1	–	13
	1933	–	–	–	2	4	4	6	2	1	–	–	–	19
	1934	–	–	–	–	1	2	2	1	–	1	–	–	7
Cottus bubalis	1930		–	3	3	1	–	–	–	–	–	–	–	7
Father Lasher	1931	–	–	2	1	1	–	–	–	–	–	–	–	4
	1932	–	–	+	1	1	–	–	–	–	–	–	–	2
	1933	–	1	1	1	1	–	–	–	–	–	–	–	4
	1934	–	1	12	3	2	–	–	–	–	–	–	–	18
Liparis montagui	1930		–	+	–	+	–	–	–	–	–	–	–	+
Montague's Sucker	1931	–	–	–	–	–	–	–	–	–	–	–	–	–
	1932	–	–	–	1	–	+	–	–	+	–	–	–	1
	1933	–	–	–	1	+	–	–	–	–	–	–	–	1
	1934	–	–	–	–	1	+	–	–	–	–	–	–	1
Lepadogaster	1930		–	–	–	–	–	–	3	+	–	–	–	3
bimaculatus	1931	–	–	–	–	–	–	–	–	+	–	–	–	+
Doubly Spotted	1932	–	–	–	–	+	–	–	1	+	–	–	–	1
Sucker	1933	–	–	+	–	–	–	–	+	–	–	–	–	+
	1934	–	–	–	–	+	–	+	–	–	–	–	–	+
Lophius piscatorius	1930		–	–	–	–	1	3	–	–	–	–	–	4
Angler	1931	–	–	–	5	–	1	1	–	–	–	–	–	7
	1932	–	–	+	–	–	+	–	–	–	–	–	–	+
	1933	–	–	–	+	–	–	–	–	–	–	–	–	+
	1934	–	–	–	–	–	–	+	–	–	–	–	–	+

The Organic Metabolism of Sea-water with Special Reference to the Ultimate Food Cycle in the Sea*

By

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From the Oceanographic Institution, Woods Hole, and the Fatigue Laboratory, Harvard University.

With 5 Figures in the Text.

INTRODUCTION.

It has long been known that, of the total organic matter in the sea, the major portion is not incorporated in the cell substance of animals and plants nor even in the detritus of their decomposition, but exists in solution in the sea-water. Pütter (e.g. 1907, 1909) endeavoured to show that this dissolved organic matter plays a central rôle in the nutrition of the living organisms in the sea.

The arguments, experiments and observations *pro* and *con* regarding this important problem have been reviewed by Krogh (1931) and others (see, e.g. Bond, 1933). Krogh assembled from his own researches and those of other workers a chain of evidence which makes it appear that none of the macroscopic organisms, nor even the larger microscopic forms, can subsist to any appreciable extent on the dissolved organic matter. Bond's (1933) observations are in agreement.

There remains the question to what extent *bacteria* may utilise the dissolved organic matter in sea-water. This is of considerable importance because of the undoubted fact that bacteria may serve as food for larger organisms such as protozoa. It is known, also, that there are indeed few natural organic substances which are not attacked by some bacteria and that bacteria can extract nutriment from extremely dilute solutions of some organic compounds. How far these two statements can be combined in discussing sea-water is uncertain.

Our problem in reality is two: (1) How great are the metabolic activities of bacteria in sea-water under the various conditions of the laboratory? (2) What bacterial activities may be inferred to take place in the sea itself?

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† Fellow of the Rockefeller Foundation.

The chemical difficulties in the way of direct determination of the dissolved organic substances have been insuperable until recently, and still prevent a practicable direct measure of the degradation of the dissolved organic matter by bacteria. However, the methods of Krogh and Keys (1934) have shown that the organic matter in sea-water is generally of the order of 200 mg. nitrogen and 6 to 10 times that much carbon per cubic metre (Krogh, Keys and Christensen, 1935). The oxidation of any appreciable fraction of this by metabolic activities of organisms should be revealed by a change in the content of dissolved oxygen in the water.

The laboratory examination of the oxygen content of plankton-free sea-water under different conditions after collection is one tool we have used. A second consists in the study of the bacterial population of the water in experiments parallel to the oxygen studies. A third attack was in the direction of an effort to discover what substances, normally present in the sea, may be, by virtue of low concentration, limiting the bacterial use of the dissolved organic matter. We have studied ammonia, nitrate, nitrite, phosphate, and, to a limited degree, hydrogen and hydroxyl ions. In this category we may also place studies at different temperatures. Finally, the application of these results to the elucidation of the actual events in the sea requires consideration of the oxygen, bacterial populations, temperature, etc., in the sea-water *in situ*.

METHODS.

To remove all plankton, including nannoplankton larger than bacteria, we have used filtration in a Büchner funnel through two thicknesses of the most retentive filter paper—Whatman's No. 44 or No. 50. To give comparisons with the filtrations of other workers, we have used a single thickness of Whatman's No. 1 or No. 2 paper. The removal of all particulate matter, including bacteria, was accomplished by filtration through a Zsigmondy type collodion membrane filter. A few small samples were prepared free of colloids by ultra-filtration through a membrane filter designed by one of us (Krogh).

Oxygen determinations were made by the Winkler method, with all titrations in duplicate. In the experimental series, the procedure was carefully to fill by siphon, with preliminary flushing, a series of identical glass-stoppered bottles. These were stored in the dark under water and bottles withdrawn, in duplicate, from time to time for analysis. The duplicate results agreed to within 0·02 c.c. O_2 per litre and better in almost all cases.

Bacterial populations were estimated from agar plate counts on at least 3 plates. Several dilutions were always made so that the cells per plate were always within the range 20 to 300. The medium used was kindly supplied by Dr. S. A. Waksman. It had the following composition :

Glucose	1 gm.
Peptone	1 gm.
K_2HPO_4	0·5 gm.
Agar	10 to 15 gm.
Sea-water	1000 ml.

The plates were counted after incubation at 21 to 23° C. for 2 days and re-counted at the end of a week.

Ammonia determinations were made by the method of Krogh (1934). The reduced strychnine method of Harvey (1926, 1928) was used for nitrate, and nitrite was estimated by the Griess-Ilosvay method as used by Rakestraw (1933).*

Sub-surface samples were taken by cleaned Nansen bottles. It should be mentioned that throughout all the work meticulous pains were taken to prevent any kind of contamination.

In many cases the filtration was quickened by vacuum. The water was always subsequently thoroughly aerated by shaking over a period of 15 minutes or more. In low temperature experiments both water and bottles were pre-cooled before bottling and storage. This is necessary if the formation of air bubbles in the bottles due to cooling and the contraction of the water is to be avoided.

Oxygen Consumption of Stored Sea-water.

It has long been known that when sea-water is stored out of contact with the air in the dark there is a diminution in the oxygen content. In most cases, however, either the water was not carefully filtered (see, e.g., Knauthe, 1898)—it should be borne in mind that single filtration removes only a portion of the smaller plankton—or the exclusion from the air was brought about by a layer of oil (e.g. Winterstein, 1909), or other possible sources of error were not excluded.

We found, similarly to Gran and Ruud (1926) and Föyn and Gran (1928), that when fresh sea-water is brought into the laboratory and stored at 20 to 23° C., there is a rapid bacterial development and reduction of oxygen content. Figure 1 gives the results of two experiments with water from Woods Hole Harbour. The " respiration " in the doubly filtered water was considerably less than in the raw water, but in both cases the oxygen removal was rapid in the first 2 or 3 days and thereafter slower, being very slow indeed after 10 or 15 days.

True ocean water behaves similarly. Experiments with water collected

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* We are indebted to Mr. Henry Mahnke for making the nitrate and nitrite analyses.

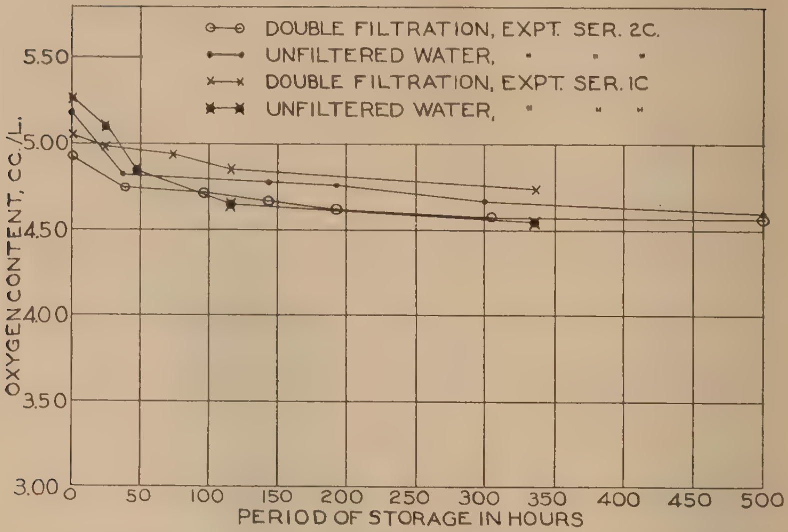

FIG. 1.—" Respiration " of sea-water stored in the dark at 20 to 23° C. Water from Woods Hole Harbour.

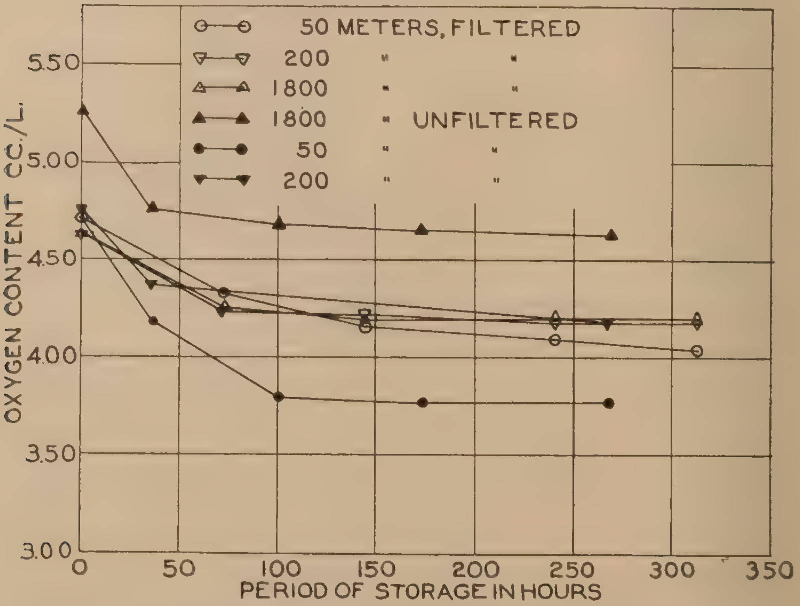

FIG. 2.—" Respiration " of true ocean water stored in the dark at 21 to 23° C.

at various depths at the 1000-fathom line south of Martha's Vineyard are summarised in Figure 2. Some differences in the "respiration" of waters from different depths appear; respiration of the water from within the photosynthetic zone is considerably more active than in the deeper water.

In Figure 3 is given the respiration observed in three series of experiments carried out under identical conditions with waters from Woods Hole, Martha's Vineyard and the open ocean respectively. The initial oxygen content in all these was between 4·8 and 5·2, and they have all been corrected to a standard initial value of 5·00 c.c. to facilitate comparison. Here, as in all our experiments, it is clear that a large fraction of the total respiration of raw water must be ascribed to the decomposition of contained plankton. And here also both filtered and unfiltered waters from 50 metres' depth show the highest respiration.

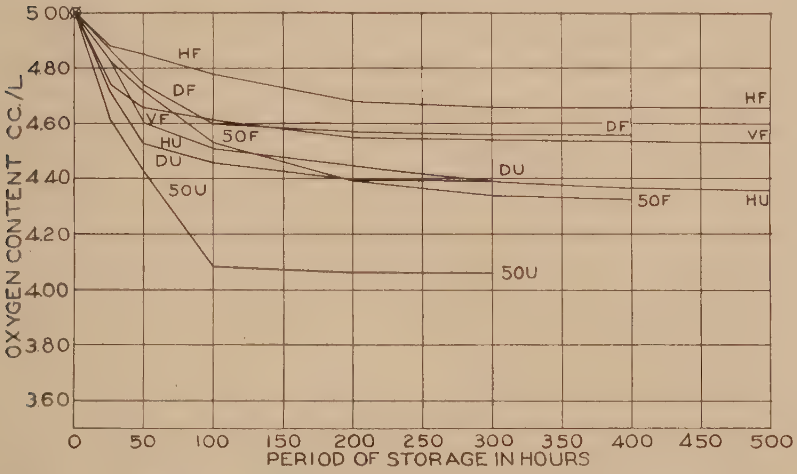

FIG. 3.—"Respiration" of various sea-waters stored in the dark at 21 to 23° C. HF= filtered Woods Hole Harbour water, UF=the same unfiltered, VF=filtered water from Vineyard Sound. 50F=sea-water from the open sea, 50 metres' depth, filtered; 50U=the same unfiltered. DF=water from the same station as 50 F but from a depth of 1800 metres, filtered; DU=the same unfiltered. Water from 250 metres at the same station behaved so nearly exactly alike DU and DF that the values are not given in this figure.

Discussions by previous workers on this subject have been based on the belief that simple filtration produces a filtrate which is "plankton-free." Although Lohmann (1908, 1911) in particular recognised the fact that nannoplankton largely escape in ordinary filtration, the fact that the nannoplankton forms a large fraction of the total mass of plankton has not been sufficiently recognised. Allen (1919) concluded that Lohmann's estimates for the nannoplankton were far too low owing to the inefficiency of the centrifuge method of separation. Bond (1933) found that of the total mass of plankton the nannoplankton may average a third and at certain seasons may represent an even greater fraction of the total. With this in mind we adopted the double filtration technique described in the " methods " section of this paper, and comparison experiments indicate to how great an extent ordinary filtration may err in producing " pure " sea-water.

In Table I are compiled the average respirations in filtered water prepared by filtration through a single thickness of ordinary filter paper and by our double filtration method.

TABLE I.

Oxygen Consumption in Oceanic Water Singly and Doubly Filtered.

Series A at 5° C. throughout, Series B at 21–22° C. Consumption in cubic millimetres O_2 per litre for the indicated period.

	Series A.					Series B.	
	0 to 100 hrs.	100 to 200 hrs.	200 to 300 hrs.	300 to 400 hrs.	400 to 500 hrs.	0 to 100 hrs.	100 to 200 hrs.
Single filtration	60	90	110	20	10	490	50
Double filtration	30	40	50	20	10	370	60

It is obvious that when filtration methods less efficient than ours are used a very large fraction of any total respiration observed subsequently must be ascribed to the decomposition of nannoplankton.

The Effect of Temperature on Sea-water " Respiration."

A striking difference in the respiration of sea-water stored at low and at ordinary temperature is apparent in Table I. This difference is consistently observed and is illustrated in Figure 4, which gives results from experiments with harbour water (Woods Hole) and inshore water (Vineyard Sound). Especially is the initial respiration very much greater in the warmer water. Whether eventually the total respiration in the cold and in the warm water would reach the same level is uncertain ; up to 3 or 4 weeks the difference is still maintained.

In water from the deep ocean we observed an interesting and perhaps significant phenomenon. When water was collected from several thousand metres' depth and never allowed to warm up, the oxygen consumption was much less than in some of the same water which warmed to 22° C. for only a few hours and then was cooled to the same level as the other water. In 2 experiments of this sort we found that in 450 hours' storage at 5 to 6° C., water which had never been allowed to rise above 7° before the experiment showed less than half the oxygen consumption of another portion of this water which had risen to room temperature for a few hours on board ship. Water collected from 2000 metres, doubly filtered and stored at 5 to 6° C., which had never been allowed to warm during any of the operations, showed a total respiration of less than 0·02 c.c. per litre in 150 hours.

It appears, then, that even temporary warming has a marked effect in producing conditions favourable to bacterial development and chemical decomposition in sea-water. This is one factor which is important in the attempt to study the organic matter of the sea by laboratory experiments.

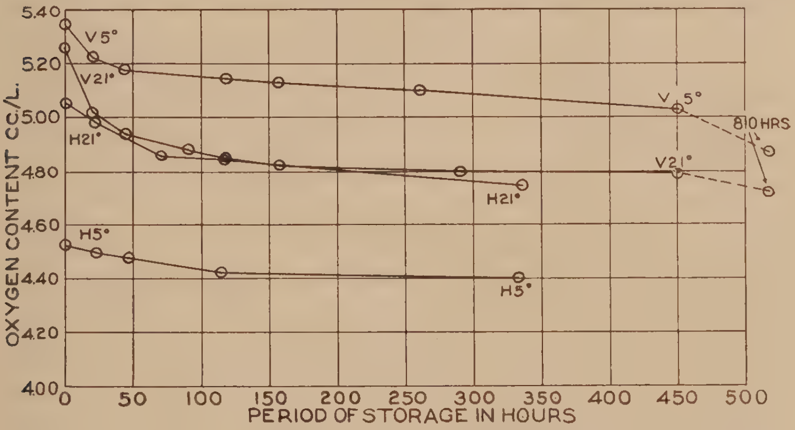

FIG. 4.—" Respiration " of sea-water from Woods Hole Harbour and from Vineyard Sound stored at 5° and at 21°. V refers to Vineyard Sound water, H to Woods Hole Harbour water.

THE BACTERIAL POPULATION.

Early studies on the bacterial population of various sea-waters *in situ* showed that the numbers decrease very abruptly with the distance from shore (Russell, 1892, 1893), and this finding has been confirmed by many workers (see Benecke, 1933). Reuszer (1933) found numbers ranging from a few hundreds per c.c. down to almost zero in waters a few miles south of Cape Cod. In the open sea, 50 miles or more from land, it appears that at all depths fewer than 100 cells per c.c. will develop on plating. Direct microscopic examination of sea-water reveals two or three hundred times as many bacteria (Cholodny, 1929; Rasumov, 1932; Waksman and Carey, 1935); it seems, however, that the number of cells viable on agar plates is roughly proportional to the total.

A remarkably rapid increase in bacterial numbers follows withdrawal of a sample of sea-water from the sea. Typical results obtained from inshore water are shown in Figure 5.

Results qualitatively similar to those given in Figure 5 were obtained in a large number of experiments. In each case a maximum bacterial population was found in 3 or 4 days at 21°, and at 5° the maximum was not reached for several weeks. However, the bacterial counts from experiment to experiment showed greater variation than did the oxygen consumption in the experiments discussed in the preceding sections. This prompts the question—to what extent is the bacterial population, either the total numbers or the rate of increase, reflected in the oxygen consumption ?

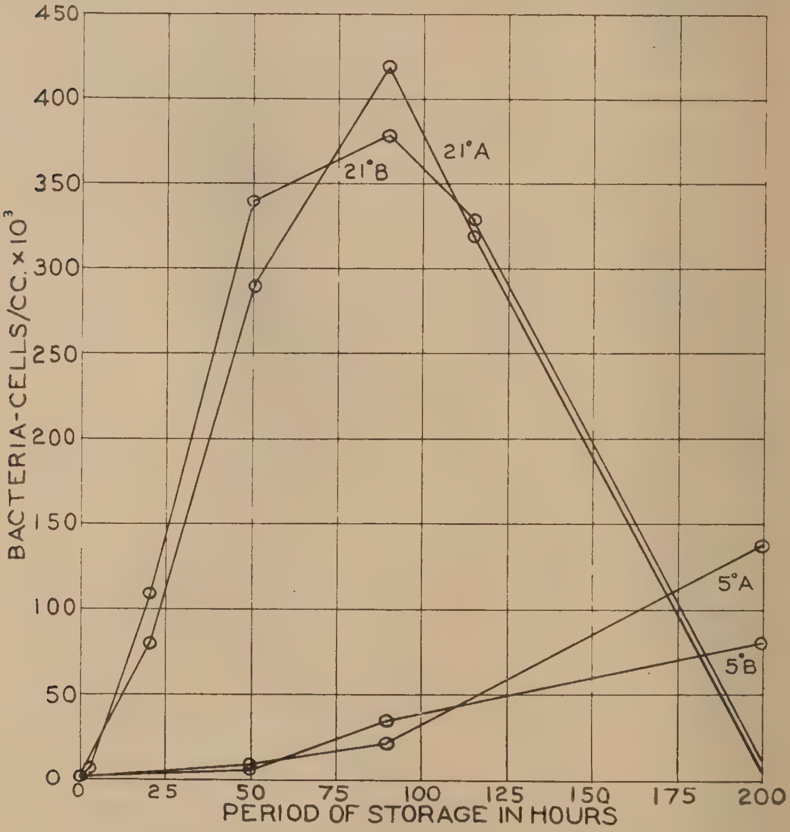

FIG. 5.—Development of bacteria in sea-water stored in the dark at 5° and at 21° C. Plate cell counts.

In our experiments, at least, there was only the crudest indication of a relation between bacteria and oxygen consumption. When the bacterial counts are high, the oxygen generally disappears more rapidly than when only few bacteria develop on the agar plates. Table II illustrates results from two parallel experiments with harbour water and may be taken as typical.

TABLE II.

Relation between Bacterial Development and Oxygen Consumption in stored Sea-water.

A refers to the first experimental series, B to the second.

Time Period.	Sample.	Temp.	O_2 used in c.c.	Average cells/c.c.	Increase cells/c.c.	O_2 uptake per 100,000 cells, per 100 hrs.	O_2 uptake per 100 hrs. per increase of 100,000 cells.
0 to 50 hours	A	5°	0·18	2,600	3,210	13·8	11·6
	A	21°	0·32	170,000	337,000	0·38	0·18
	B	5°	0·17	1,400	1,960	24·2	17·4
	B	21°	0·34	147,000	294,000	0·50	0·22
50 to 115 hours	A	5°	0·03	20,000	18,000	0·23	0·26
	A	21°	0·11	360,000	130,000	0·05	0·12
	B	5°	0·04	37,000	34,000	0·17	0·18
	B	21°	0·05	360,000	40,000	0·02	0·18

In sterile experiments, the oxygen content of the stored water was not always constant, but the maximum " consumption " was never more than 0·05 c.c. no matter how long the samples were stored.

It was a constant peculiarity that in the first few days in low temperature experiments, the respiration, though small in total, was always very large per unit of viable cells. Unless the plating methods give a grossly erroneous picture, the results seem to indicate that bacterial respiration proper can be responsible only for a fraction of the oxygen used up, while the rest which disappears fairly rapidly, even at low temperature, must be accounted for in some other way.

In two experiments small amounts of sea-water were prepared, by ultrafiltration, free of all particulate matter, including colloids. These samples were inoculated with non-sterile sea-water and bacterial counts made from time to time. The multiplication of bacteria in this water was at least as great as in ordinary filtered water. The samples were too small to permit studies of the oxygen contents.

Influence of Added Ammonia and Phosphate.

In a large number of the experiments ammonium sulphate was added to portions of the water to give a final concentration of 50 to 75 gammas ammonia nitrogen per litre (i.e. 3 or 4 times the control). In almost all cases there was no effect on either oxygen consumption or bacterial growth.

In a few cases there was an indication of a depressant effect, but this was so slight as to be doubtful. Clearly the changes in the sea-water are not, in these experiments, limited by lack of available nitrogen.

The addition of dipotassium phosphate in amount equivalent to 100 gammas phosphate per litre had little or no effect in experiments with deep ocean water (which has naturally a high phosphate content). With harbour water, however, there was certainly an increased respiration, most marked in raw water, but also noticeable in filtered water in the first few days. Table III shows the total respiration in an experiment of this sort. Almost identical results were obtained in a duplication of the experiment.

TABLE III.

Influence of Addition of 0·1 mg. PO_4 (as K_2HPO_4) to Sea-water taken from Woods Hole Harbour.

Water stored in dark at 22° C.

Material.	Raw water.	Raw water + PO_4.	Filt. water.	Filt. water + PO_4.
Total Respiration first 100 hours.				
O_2 used, c.c./l.	0·34	0·69	0·23	0·32
Total Respiration first 500 hours.				
O_2 used, c.c./l.	0·70	1·30	0·38	0·52

Alterations in Ammonia in Stored Sea-water.

The oxygen consumption and bacterial development observed in the present experiments indicate metabolic processes which would be expected to involve also nitrogen compounds. Two diametrically opposed expectations could be developed theoretically. It would seem reasonable that in the bacterial development ammonia, as an easily available form of nitrogen, would be used and therefore the ammonia content of the water would diminish. Equally reasonable would be the expectation that the bacterial activity in decomposing complex organic substances in solution in sea-water would liberate a certain fraction of the nitrogen as ammonia, and hence the stored water would show an increase in ammonia concentration. In actuality, neither of these possibilities is realised generally to a preponderant degree, and it would seem that both types of nitrogen metabolism take place in sea-water.

The more frequent behaviour of the ammonia concentration is to diminish on storage, especially when the initial value is high. In Table IV are assembled results showing this phenomenon.

TABLE IV.

Ammonia Concentration of Stored Sea-water, in mg. NH_3–Nitrogen per Cubic Metre.

Experiments on board the *Atlantis* in the Gulf of Maine, September, 1933. Storage at 5° C. in dark. Sterile series by mercuric chloride (1/10,000); sterility checked by plating.

Sample.				
A	Time, hrs.	2·5	8·5	290
	NH_3 γlitre	23	19	8
B	Time, hrs.	6	18	90
	NH_3	49	28	23
C	Time, hrs.	1	7	290
	NH_3	39	41	10
A	Time, hrs.	2	9	290
sterile	NH_3	22	16	8
B	Time, hrs.	6	18	90
sterile	NH_3	44	32	27

The decreases in ammonia in the sterile series show that a purely chemical reaction is involved. Similar reduction in ammonia in sterile sea-water was observed by Kreps (1934), who also found, as we did, that the ammonia concentration in stored sea-water behaves in anything but a consistent fashion from experiment to experiment. Table V following contains results which illustrate other types of behaviour.

TABLE V.

Ammonia Concentration of Stored Sea-water, in mg. NH_3–Nitrogen per Cubic Metre.

Water from Vineyard Sound, August, 1934. Storage in dark under water. In the A series the water was merely filtered free of plankton, in the B series ammonium sulphate was added initially. The temperatures are those at which storage took place. All values are averages of several analyses.

Time (hrs.).	1	20	54	111	204
A, 5°	18	—	30	21	17
B, 5°	54	—	40	32	27
A, 21°	18	11	6	21	27
B, 21°	54	44	25	39	35

The presentation of further data on ammonia concentrations in stored sea-water would only emphasise the fact that the phenomena are complex and are not as yet capable of precise interpretation. It should be pointed out, however, that in sea-water sterilised by filtration and stored in the dark at 20–22° C., ammonia liberation occurred in both our series of experiments of this kind, one of which is given in Table VI.

TABLE VI.

AMMONIA IN FILTRATION-STERILISED SEA-WATER FROM WOODS HOLE HARBOUR STORED IN DARK AT 20–22° C.

Time in hours.	3	20	72	115
NH_3, mg. N/cu. metre	10, 10	16, 17	21, 26	24, 26

Attempts to follow other forms of nitrogen reveal no changes of significant magnitude to throw light on the nitrogen transformations in stored sea-water. The experimental data summarised in Table VII are typical.

TABLE VII.

NITROGEN COMPOUNDS IN SEA-WATER, ALL VALUES IN TERMS OF MG. N PER CUBIC METRE.

Water from Vineyard Sound, filtered and stored at 8° C. in the dark. Series B with added ammonium sulphate.

	NO_2.	NO_3.	NH_3.	O_2 (c.c./l.).
A, start	1·3	55	18	5·23
A, 100 hrs.	1·1	52	20	5·14
B, start	2·2	55	45	5·24
B, 100 hrs.	2·2	54	31	5·12

It appears to us that the only conclusion that can be drawn with regard to nitrogen metabolism in stored sea-water is that there are usually a number of forces at work, some operating to reduce the free ammonia, others tending to release ammonia ; the observed ammonia concentration will always be a resultant of these forces, and the predominating action will be dependent, among other things, on the temperature, the varieties of bacteria present, and the chemical nature of the organic substances in solution, if this is variable.

DISCUSSION.

The bacterial development and the oxygen consumption observed in the present experiments can only have proceeded at the expense of organic nutriment gained from the dissolved matter in the sea-water. The amount of dissolved organic matter used in this way cannot be estimated except by making assumptions with regard to the RQ (ratio of carbon dioxide produced to oxygen consumed) characterising the bacterial metabolism, but it is not insignificant.

From analogy with aerobic bacteria in general, an RQ between 0·5 and 1·0 would be reasonable to ascribe to the mixed marine bacteria with which we are concerned. While it must be emphasised that we have no direct estimate for the true RQ, it may be illuminating to apply the best figure we can suggest on the basis of knowledge of the RQ of other forms and thereby calculate a *possible* figure for the amount of dissolved organic matter degraded in one of our typical experiments. In the experiment A 21° (see Table II) the total oxygen consumption per litre of sea-water in 115 hours was 0·43 c.c. at N.T.P. (760 mm. Hg and 0° C.). Assuming an RQ of 0·85 this would mean that $0{\cdot}85 \times 0{\cdot}43 = 0{\cdot}36$ c.c. CO_2 was produced. But 1 litre of CO_2 at N.T.P. weighs 1·96 grams so there has been produced 0·71 mg. CO_2. This means that in each litre $\frac{12}{12+2(16)} \times 0{\cdot}71$ or 0·19 mg. carbon has been degraded from dissolved organic complexes by the bacterial metabolism. Since the total dissolved organic carbon is of the order of 2 mg. per litre, roughly 10 per cent has been decomposed.

Similar calculations for our various experiments indicate that up to something like 10 or 15 per cent of the total dissolved organic matter was destroyed.

This much of the total dissolved organic matter, then, is readily susceptible to biological degradation, provided the stimulus of handling the sea-water in the laboratory is supplied. That such a “ stimulus ” is necessary is shown by the fact that, in the sea, neither the bacterial multiplication nor oxygen consumption can be observed to take place. It may be possible, of course, that in the sea protozoan populations keep pace and by feeding on the bacteria restrict them to small numbers. More likely would it be that there is always only a very small bacterial activity in pure sea-water owing to the extreme stability of the ocean as a chemical and physical environment.

It is certain that sea-waters of great variety—we studied harbour, inshore, offshore, and open ocean sea-water from depths of 1 to 2000 metres—all possess a great reserve of potential nutriment which suddenly comes into service when what seem to be very small alterations in the system are introduced. It is uncertain where this energising action takes place, in the chemical nature of the organic complexes or in the bacteria themselves, but without it the metabolic activities would at least proceed at a far slower rate.

The fact that the burst of metabolic activity observed in the sea-water is always self-limiting may be interpreted in either of two ways. One possibility is that the bacterial development stops because the bacteria produce metabolites which are eventually toxic to them. The other possibility is that the bacterial metabolism ceases because only a small fraction of the total dissolved organic matter is available. In support of this latter suggestion is the fact that addition of small amounts of a great variety of organic substances results in a much greater bacterial activity. This is evident from our experiments with unfiltered water and has been demonstrated in experiments at Woods Hole by Dr. S. A. Waksman who studied the effect of addition to sea-water of a great variety of organic compounds.

The bacterial activity is ordinarily not limited by nitrogen want, but if pure carbohydrates are added to sea-water the bacterial metabolism ceases at a point where, although two or three times as much oxygen is consumed as without the carbohydrate, there is still a plentiful reserve of both carbohydrate and oxygen. The further addition of small amounts of nitrogen in any form with the amino linkage is followed by continued bacterial activity until all the oxygen is used up from the sea-water.

All this makes it seem likely that the principal limitation to bacterial development in pure sea-water is lack of *available* organic carbon, and that some of the dissolved organic matter can satisfy this want if the physical characteristics of the environment are slightly altered for a time. It is not improbable that this happens in the sea at various times and places, but that, in general, an equilibrium is maintained in which only a minimal bacterial population is supported by the dissolved material which comes to be, perhaps not wholly out of organic circulation, but certainly not ordinarily a major link in the ultimate food cycle in the sea.

SUMMARY.

Studies are reported of the behaviour of stored sea-water with regard to oxygen, ammonia, and bacteria content in relation to the conditions of storage and to the effect of various filtration procedures.

When sea-water is sterilised by filtration and stored in the dark, the oxygen content remains constant or diminishes only by less than 0·07c.c. per litre in several hundred hours.

In non-sterile experiments there is always an oxygen consumption roughly parallel to a bacterial multiplication which begins very suddenly

after collection of the water. These effects are greatest in "raw" water, less in paper-filtered water and least in water which is doubly filtered.

These metabolic activities are self-limiting and stop when there is still a large reserve of ammonia and oxygen and when only a small fraction of the dissolved organic matter has been decomposed.

The behaviour of the ammonia content in these experiments indicates that the ammonia content observed in sea-water is a resultant of purely chemical actions tending to diminish the ammonia and of biological forces in which both ammonia production and ammonia liberation by bacteria may be observed.

Great bacterial development may take place in sea-water freed of *all* particulate matter including colloids.

It appears that in the sea there is generally an equilibrium such that only minimal bacterial activity at the expense of dissolved organic matter may take place, but that very small changes in the system may make available for bacterial metabolism perhaps 10 or 15 per cent of the total dissolved organic matter.

Bacterial activity in sea-water is very sensitive to temperature and to alkalinity and relatively independent of ammonia, nitrate or nitrite and also oxygen above half-saturation. Lack of phosphate may on occasion be a limiting factor.

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The Rate of Liberation of Phosphate in Sea Water by the Breakdown of Plankton Organisms.

By

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With One Figure in the Text.

In the late spring of 1934 four experiments were started to determine how quickly inorganic phosphate may be set free from plankton. Samples of plankton caught in fine and very fine silk tow-nets were analysed for phosphorus (Cooper, 1934) and aliquot parts were filtered on a silk disc having 200 meshes to the linear inch. The plankton was then added to two litre samples of fresh outside sea water in Winchester quart bottles. In all cases the amount of plankton initially present in the sample of sea water was less than 3% of that added.

In each experiment a sample of sea water untreated except for passage through butter muslin was kept as a control. The Winchester bottles, except in Experiment 1, were wrapped in black paper and all were stored in a cupboard away from light and shaken by hand at intervals. The mean temperature of the storage cupboard was about 14° C. in April, 16° C. in May and 19° C. in June. At suitable times 100 ml. portions were removed from the well-shaken bottle and analysed for phosphate in the usual way (Denigès-Atkins method), except that samples enriched with plankton had first to be filtered through Zsigmondy membrane filters (filtration time, 20 seconds). Even so after a few weeks the colour match with standards in the phosphate analyses on these filtrates was not too good and the analyses are less accurate than those on ordinary sea water. The worst samples to compare were those rich in plants. All results are recorded as mg. P. per cubic metre corrected, when necessary, for salt error.

Experiments 1 *and* 2. *Zooplankton.*

The sample of plankton used for Expt. 1 was mixed, consisting mostly of animals. That for Expt. 2 contained Calanus, some Acartia and Temora, a few Ctenophores and very little plant life.

The control to Expt. 1 after two months reached a maximum phosphate content greater than the preceding winter maximum in the

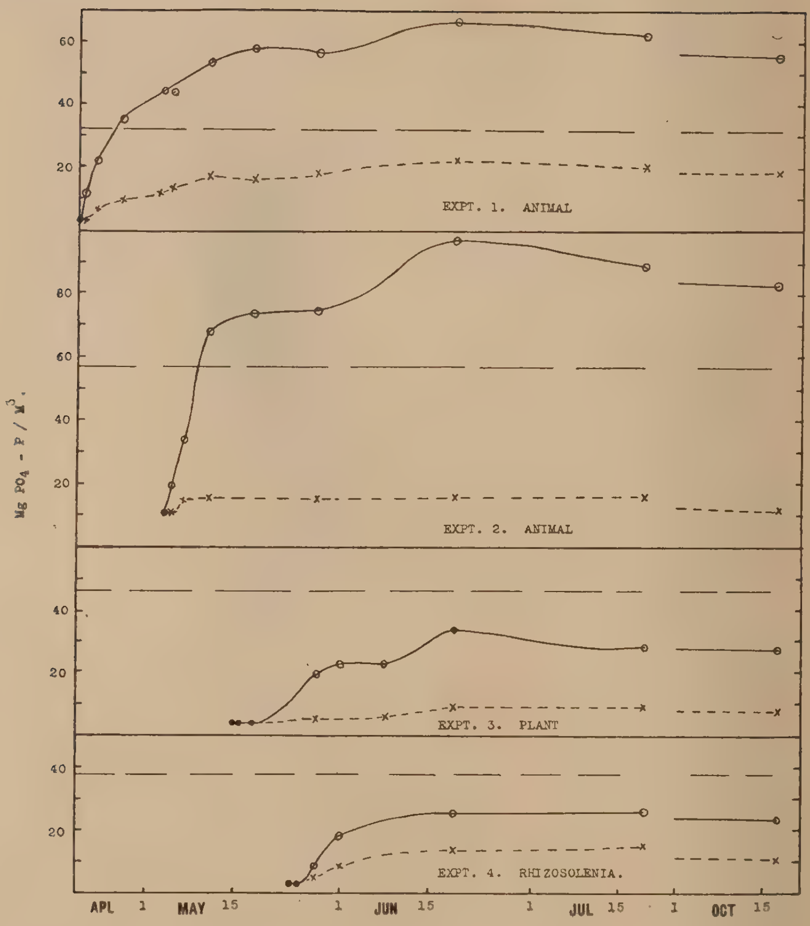

FIG. 1.—Liberation of Phosphate-phosphorus (PO_4–P) by breakdown of plankton.

- - - - - - - - - - -	Controls.
————————	With added plankton.
——— ———	Sum of PO_4–P initially present in the water and plankton–P added.

English Channel. In the control to Expt. 2, however, the liberation of phosphate was much less. In the waters with added zooplankton (Expt. 1, 29 mg. and Expt. 2, 46·5 mg. per cubic metre of added phosphorus) the liberation of phosphate was very rapid, about 10 mg. P being set free in the first twelve hours and an amount equivalent to that added as plankton in about six days. Quite unexpectedly phosphate continued to be set free until the maximum was reached after about six weeks or two months. It was clear that about 40 mg. P per cubic metre was being rapidly set free from dissolved organic compounds present in the sea water. The results of Matthews (1917), Ibañez (unpublished), Kalle (1933) and Kreps (1934) show that sea water may contain 30–50 mg. of organic phosphorus per cubic metre which, however, may include some arsenic (Atkins and Wilson, 1927, and Rakestraw and Lutz, 1933).

Experiments 3 *and* 4. *Diatoms.*

The sample used for Expt. 3 was rich in diatoms, particularly Rhizosolenia spp. That for Expt. 4 was practically entirely diatoms; each litre of the experimental water contained 453,000 *Rhizosolenia shrubsolei*, 90,000 *R. fäeroensis*, 28,000 *Skeletonema costatum*, and 6,200 *Guinardia flaccida*, equivalent to, say, 570,000 *R. shrubsolei*. Little else was present. I am indebted to Dr. Lebour for these counts made with the hemacytometer.

The control to Expt. 3 showed little change, but that to Expt. 4 in a month showed a rise of 12 mg. P per cubic metre. In the experiments with diatoms added, little happened for two or three days, in marked contrast to the behaviour of animal plankton, and then rapid liberation of phosphate took place, the maximum being reached in a month. Even at the maximum only part of the phosphorus added as phytoplankton had been set free to the water.

Two phenomena are common to most of the curves in Fig. 1. Firstly, an inflection is to be noted after 15–20 days' storage. The rate of liberation slowed down and then picked up again before reaching the maximum. Secondly, a slow fall in phosphate occurred in the four months after the maximum had been reached. No explanation is apparent for this, although moulds may play a part. The experimental waters were much richer in plankton than the sea ever is, so that presumably compared with natural conditions all processes of decay were much accelerated. A number of other experiments made under somewhat different conditions with the same catches of plankton served but to confirm the results here set forth.

The author is indebted to Mr. H. W. Harvey for suggesting this research and for his interest in its progress.

TABLE I.

All Phospate Data as mg. P per Cubic Metre corrected for Salt Error.

				Increase in PO$_4$–P due to breakdown.		Minimum amount of PO$_4$–P set free from original sea water.
Expt.	Date started 1934.	Initial PO$_4$–P in water.	P in plankton added.	Control.	With added plankton.	
Zooplankton :						
1	20/4	3	29	19·5	64	35
2	4/5	10·5	46·5	5	87	40
Phytoplankton :						
3	15/5	5	46	5	30·5	—
4	24/5	2·5	35	12·5	24	—

SUMMARY.

Samples of animal and plant plankton were added to sea water in glass vessels and the subsequent changes in the phosphate content of the water were followed.

The breakdown of the zooplankton was very rapid and more phosphate was set free than had originally been added as plankton. The balance was produced from dissolved organic phosphorus compounds in the water. The breakdown of phytoplankton showed a short time lag and only a part of the phosphorus added was set free as phosphate.

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A Note on Manganese in Marine Plankton.

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Although to many organisms manganese is known to be of great importance (Berkeley, 1922; Brenchley, 1927; Hopkins, 1930) its part in the economy of the sea is unknown. Some attempts were therefore made in 1934 to estimate the manganese in marine plankton using the residues from the determinations of phosphorus (Cooper, 1934; Harvey *et alia*, 1935). The residues from the triplicate digests from each cruise were combined and concentrated from about 200 to 70 ml. The concentrates were then examined quantitatively for manganese by the periodate method of Willard and Greathouse as described by Yoe (1928). In all cases but one the concentration of manganese was less than could be detected with certainty (Table I). In the absence of confirmatory data the figure of 5γ per litre of the diatom catch of May 15th must be regarded as suspect and attributable to chance contamination. Thus in these catches at L4 (5 miles off shore) during the spring outburst in 1934 manganese amounted to less than three parts per million million parts of water filtered, equivalent to one-thousandth or less of the phosphorus content.

TABLE I.

Manganese content of plankton caught at Station L4. First group caught with quantitative net; second group with ordinary tow-nets. The diatoms of May 15th and 24th were separated from the larger animals by passage through a silk net having 60 meshes to the linear inch.

Date 1934.	Description of plankton.	Manganese in catch γ/m^3. of sea water filtered.	Ratio Mn/P (weight/ /weight).
9/3	Routine haul; mixed . .	<3	$<0{\cdot}003$
10/5	,, ,, ,, . .	<1	$<0{\cdot}0008$
15/5	,, ,, ,, . .	<2	$<0{\cdot}002$
23/5	,, ,, ,, . .	$<0{\cdot}5$	$<0{\cdot}002$
10/5	Fæcal pellets . . .	$<0{\cdot}3$	$<0{\cdot}02$
		γ/litre of catch.	
4/5	Animal plankton . .	$<0{\cdot}2$	$<0{\cdot}0008$
15/5	Diatoms	ca 5 (?)	ca 0·01 (?)
24/5	Rhizosolenia spp. . .	<2	$<0{\cdot}02$

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The Ecology of a Salt-Marsh.

By
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With 17 Figures in the Text.

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INTRODUCTION.

It has long been known that most aquatic animals are sensitive to alterations in their environment, and that relatively small changes in the composition of the surrounding medium will cause serious physiological disturbances.

Earlier workers showed that many marine animals have body fluids which are approximately isotonic with sea water, and that dilution or concentration of the surrounding medium causes corresponding changes in their blood, and swelling or shrinkage of their tissues. Recent work, however, has shown that this is not true for all marine animals, but that certain of them can, to some extent, control the osmotic pressure of their body fluids. Those which can do so are able to survive in water of varying salinity, a few living as well in fresh water as in salt.

The means by which this is brought about are being investigated by an increasing number of workers, and the parts played in the regulatory mechanism by other factors in the environment, such as oxygen tension, hydrogen ion concentration, calcium content, are gradually being brought to light.

This tolerance of changes in the external medium is of special importance to animals attempting to colonise brackish-water habitats such as salt-marshes and estuaries, where the conditions of salinity in particular are continually fluctuating. In view of the attention that the problem is receiving at the present time, an investigation into the conditions in one type of brackish-water habitat, a salt-marsh, was begun. Owing to other work a complete record of conditions throughout the year could not be made, but it is hoped that sufficient data have been obtained to give a fairly accurate picture of the range of variation in the pools.

I wish to record my thanks to Professor J. H. Ashworth, F.R.S., in whose department the work was carried out, and particularly to Professor A. D. Hobson of Armstrong College, Newcastle-upon-Tyne, whose constant help and encouragement were of the greatest assistance at every stage of the work. I am also indebted to Dr. K. G. Blair, Dr. W. E. China, Dr. F. W. Edwards and Miss S. Finnegan, of the British Museum of Natural History, for the identification of the Coleoptera, Hemiptera, Diptera and Arachnida, and to Dr. P. Gray, of the Department of Zoology at Edinburgh, for the identification of the Copepods.

LITERATURE.

Papers on the fauna of brackish water are numerous, but few of them are concerned with salt-marshes.

Hickson (1920) describes the occurrence of *Protohydra leuckarti* near Southampton, and mentions a few associated animals from the pools.

Robson (1920) gives details of the distribution of two species of Hydrobia in an Essex marsh.

Lambert (1930) gives a list of the species of animals found in the marsh ditches of the Thames estuary.

Ellis (1932) describes the fauna of a number of brackish ditches and pools in Norfolk. A few isolated observations on the conditions in the pools are given.

Lundbeck (1932) gives a detailed list of the fauna found in an extensive series of shallow lagoons and pools in North Germany.

Sick (1933) describes the distribution of a large number of species in certain brackish-water ditches in North Germany. He gives a few observations on the salinity and hydrogen ion concentration, and discusses the fauna of the ditches in relation to that of the adjacent part of the Baltic. He has also drawn up a table of species found in brackish waters in Northern Europe.

Nicol (1933), in a preliminary account of certain salt-marshes in Northumberland, gives a short list of species found in the pools, along with isolated observations on the hydrogen ion concentration and salinity.

Kevan (1934) describes a salt-marsh at Tynninghame in East Lothian, and gives a list of animals in it associated with a new variety of *Limopontia depressa.*

The following papers contain details of the fauna of larger areas of brackish water and of estuaries.

Johanssen (1918) gives an account of the fauna of the Randers Fjord carefully correlated with the salinity of the different regions.

Redeke (1922), in a monograph on the flora and fauna of the Zuider Zee, gives a short account of the hydrographical conditions and a detailed account of the species found.

Willer (1925 and 1931) compares the hydrography and fauna of the Frische Haff from the point of view of fisheries, with the conditions and fauna of a similar, though salter, body of water—the Kurische Haff—in the same neighbourhood.

Segerstrale (1934) describes the hydrography and changing conditions in several small arms of the Baltic, and correlates the fauna with the conditions.

The following papers are concerned with the fauna of estuaries.

Stammer (1928) gives an account of the fauna of the mouth of the Ryck.

Percival (1928) describes the fauna of the Rivers Lynher and Tamar.

Alexander (1930–31) gives a list of the species found in the estuary of the Tay.

The only detailed work on the conditions in salt-marsh pools is that of Gessner (1932), who made a series of observations at midnight and mid-day on the oxygen content, hydrogen ion concentration, temperature and " hardness " of the water. He found that at midday oxygen, pH and temperature are at a maximum, while the carbon dioxide and " hardness " are at a minimum, while the reverse is the case at midnight. The pools in which the observations were made were filled with dense masses of *Ranunculus baudottii.*

METHODS.

A series of pools was chosen for investigation covering as far as possible the range of conditions which might be expected in the marsh, by reason of their position, nature of the bottom, presence or absence of algæ and diversity of fauna, and a record of conditions was kept for considerable periods of time, under widely different weather conditions. The marsh was visited at least twice a week, and the following factors investigated.

(*a*) Salinity.
(*b*) Oxygen content.
(*c*) Alkali reserve.
(*d*) Hydrogen ion concentration.
(*e*) Temperature.

The hydrogen ion concentration and the temperature were recorded in the field. For the other determinations two sets of water samples were taken, one from the surface and one from immediately above the mud at the bottom of the pool. The water intended for oxygen determinations was pipetted slowly from the pool and run into bottles of about 100 c.c. capacity. At all stages of the process the water was isolated from the air by a layer of liquid paraffin. At the same time a second set of samples was taken for salinity and alkali reserve determinations. The oxygen content was measured by Winkler's method, the alkali reserve by titration with hydrochloric acid after boiling off the carbon dioxide, and the salinity by titrating with silver nitrate.

Samples of mud from the bottoms of pools for estimating the chlorine content of the contained water were obtained by forcing a brass tube of one square inch in cross section into the mud to the required depth, corking the upper end and withdrawing the tube with a column of mud. This was then pushed out, cut up into lengths and placed in separate containers for transport. Each sample was weighed, dried, re-weighed to get the volume of contained water, and washed free from salt with distilled water. The chlorine content of the washing water was then determined, and from it that of the original volume of water calculated.

The meteorological records were obtained from the Meteorological Office of the Air Ministry, to whom my thanks are due for their kindness in supplying them. It was not possible to obtain figures for Aberlady itself, but those recorded for the rainfall at Dirleton, and for sunshine at North Berwick, three and eight miles to the east respectively, are probably sufficiently accurate.

THE MARSH.

The salt-marsh under investigation fringes the sands of Aberlady Bay on the south shore of the Firth of Forth, fifteen miles east of Edinburgh.

Owing to the flatness of the coast, when the tide recedes, two square miles of sand are left exposed for eight or nine hours at a stretch. The bay is intersected by the estuary of the Peffer Burn, which enters it at the south-east corner, and which flows, during the period of low tide, in a channel following the south shore (Fig. 1).

The saltings run as a narrow fringe round the edge of the bay. They vary in character in different parts. On the east shore the sand is clean and unmixed with mud, and the saltings are hardly raised above the level of the bay. Hollows and channels are numerous, but, because of the porosity of the soil, they drain dry in a few hours and are not refilled until the next period of spring tides. This region is relatively barren. On the south shore, however, where the mud brought down by the stream accumulates, many permanent pools are formed.

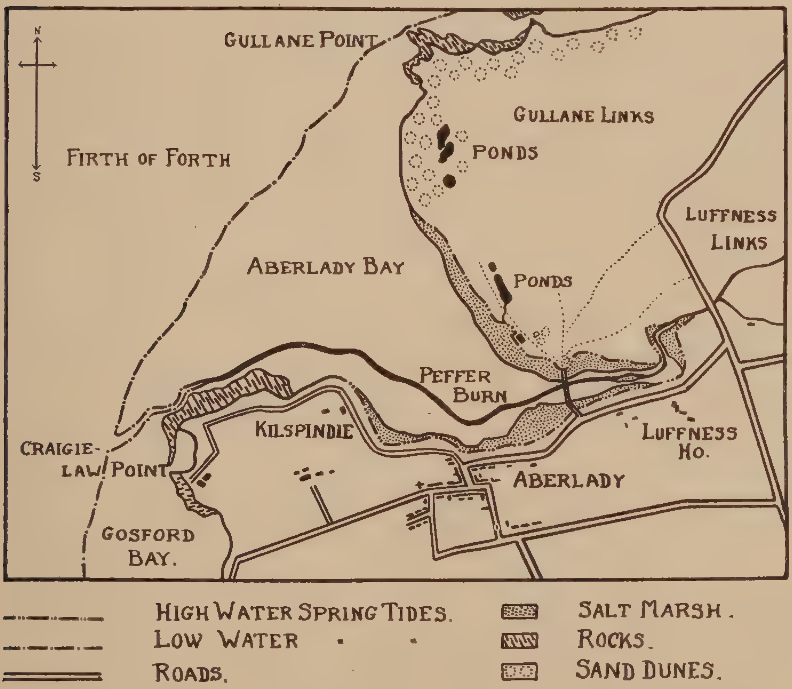
N
S
GULLANE POINT
FIRTH OF FORTH
GULLANE LINKS
PONDS
LUFFNESS LINKS
ABERLADY BAY
PONDS
PEFFER BURN
KILSPINDIE
CRAIGIE-LAW POINT
LUFFNESS HO.
ABERLADY
GOSFORD BAY.
HIGH WATER SPRING TIDES.
LOW WATER
ROADS.
SALT MARSH.
ROCKS.
SAND DUNES.

Fig. 1.—Sketch map of Aberlady Bay to show the position of the salt-marsh.

The part chosen for particular investigation lies at the south-east corner of the bay at the point where the Peffer Burn enters the sea at high tide. It is divided into two regions by the stream, the part on the right bank being about a hundred yards square, the part on the left being nearer the open sea and about six times that area (Fig. 2).

On the right bank of the Peffer the greater part of the Gullane Links consists of blown sand, but underlying this are areas of quartz dolerite, which appear on the surface on the higher parts and which dip south-west towards the bay. On the left bank, a few hundred yards inland, rocks of the lower carboniferous series underlie the soil. Immediately behind the marsh are calciferous sandstones dipping west-north-west so that water draining over these rocks might reach the marsh. Farther west, Aberlady village is situated over rocks of the carboniferous limestone series. These, however, dip west-south-west and drainage water from this area cannot affect the marsh. The soil on top of these rocks might be expected to be derived partly from them and partly from blown sand from the bay, and to be fairly limy. Between the carboniferous rocks and the shore is a strip of raised beach, which also appears on the right bank of the burn, consisting of sand and comminuted shells, and it is on this that the marsh is formed.

Besides drainage water from the hinterland, the water of the Peffer Burn affects the conditions in the salt-marsh pools. The stream rises near East Fortune in a patch of alluvial soil. It then flows for two miles over basalt, and crosses a mile of quartz trachites. The last three miles of its course are again across an alluvial plain. One tributary, the Mill Burn, rises near Dirleton, also in a patch of alluvium, and crosses two miles of quartz trachites and a mile of calciferous sandstone before reaching the Peffer Burn as it winds across the alluvial plain on its way to the sea.

On the left bank the soil of the marsh is soft and muddy, and the greater part of the surface is covered with a loose turf of *Armeria vulgaris* mixed with some *Aster tripolium*, *Spergularia marina*, *Plantago maritima* and *Triglochin maritimum.* Here and there round the edges of the lower pools *Pelvetia canaliculata* and *Salicornia herbacea* grow in quantity. *Glycera maritima* does not occur as a definite band along the seaward edge of the marsh as in so many places, but forms here a clearly-marked network in the wetter parts, marking out the old drainage systems now filled up or converted into chains of pools. The higher parts of the marsh are covered with *Festuca ovina* mixed with *Cochlearia officinalis* and *Potentilla anserina.* Round the edges of the pools *Triglochin maritimum* forms numerous tufts, and one or two patches of *Atriplex patula* are also to be found. The Festuca association is not confined to the region round high-water mark, but occurs in isolated patches on hummocks right down to the seaward edge of the marsh. This edge shows erosion by wave action where it is exposed to the north-west ; near the bridge and behind the hulks this is absent, but elsewhere the edge of the marsh is undercut, and is raised from three to twelve inches above the level of the mud of the estuary.

On the right bank the vegetation is somewhat different. Little or no erosion is taking place and irregular patches of Glycera and Salicornia are pushing their way out over the surface of the sand and increasing the area of the marsh. In the higher marsh on this side the soil is sandier and drier, and the turf is closer and composed almost entirely of *Armeria maritima*, mixed in the wetter parts with *Salicornia herbacea.* The

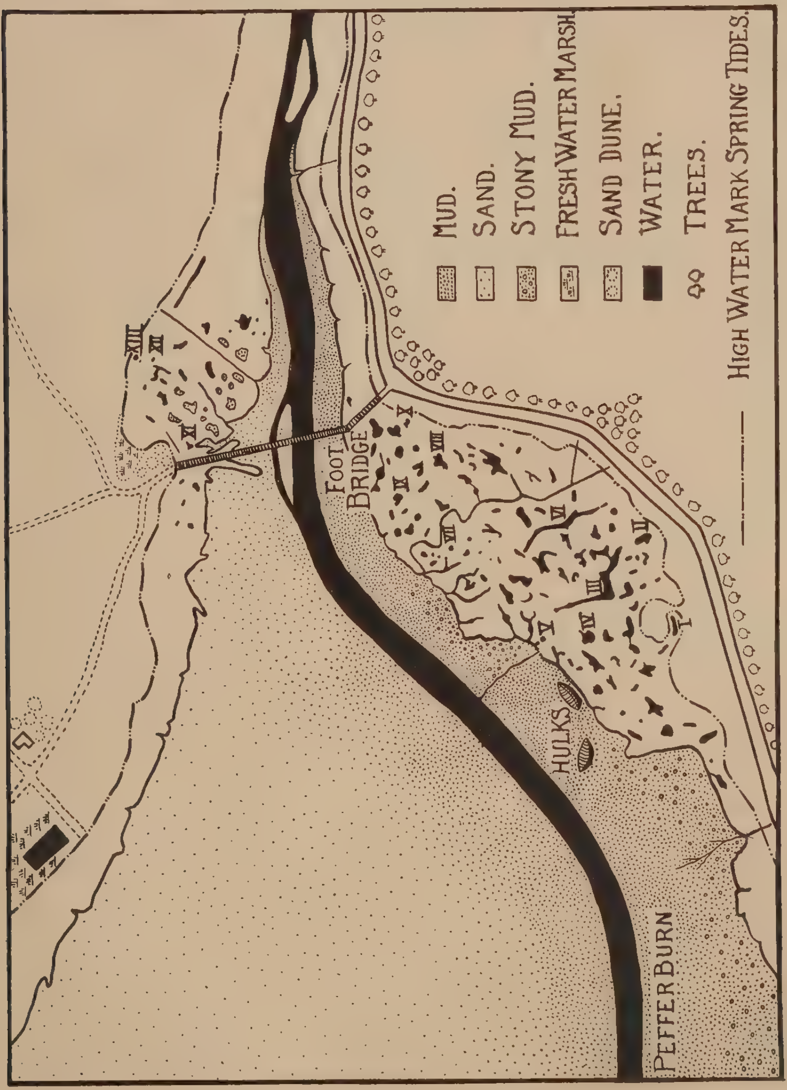
MUD.
SAND.
STONY MUD.
FRESH WATER MARSH.
SAND DUNE.
WATER.
TREES.
HIGH WATER MARK SPRING TIDES.
FOOT BRIDGE
HULKS
PEFFER BURN

Fig. 2.—Sketch map of Aberlady salt-marsh to show the position of high-water mark and the distribution of the pools.

upper edge of the marsh merges gradually into a fresh-water bog at one place and into a small sand-dune at another.

The pools are formed all over the marsh from high-water mark to the seaward edge. Unfortunately a complete transition series from marine to fresh-water conditions is not found, since both areas of marsh are terminated abruptly by a four-foot bank at their landward edge, marking an old beach level, and, although the land appears to be rising still, none of the pools has yet been completely freed from tidal influence.

The pools differ greatly in shape and size. Some are almost circular, while others are long and narrow, winding about with numerous side branches. They appear to be derived from old drainage channels which have become blocked in places by fallen banks and rubbish brought in by the tide. On the left bank the course of the channels can be clearly traced by means of the *Glycera maritima*. The area of the pools varies greatly. The smallest are not more than a square foot, while the largest are as much as twenty or more square yards in surface area. In depth they vary from three or four up to eighteen inches. As a general rule the pools near the top of the marsh are the shallowest, but there are many exceptions.

On the right bank the soil is sandy and the bottoms of the pools are firm and porous. Consequently the pools are of a less permanent character, many of them draining dry for part of the time between each group of high tides. The effects of drainage water on the conditions in the pools is also more marked on this side. On the left bank there are a few pools with sandy bottoms, but the majority have a thick layer of fine mud to a depth of eight or ten inches on top of the sand. A few pools near the foot-bridge have gravelly bottoms with large stones here and there. In the pools near high-water mark quantities of dead leaves accumulate, which decay and alter considerably the consistency of the mud.

In several places the old drainage channels have been kept open, or new straight ones cut. The water running in these is fresh.

THE FAUNA OF THE MARSH.

The fauna of the marsh can be considered under two main headings: the fauna of the surface of the marsh, and the fauna of the pools.

The Fauna of the Surface of the Marsh.

The fauna of the marsh surface can be divided into two groups: animals visiting the marsh to feed, and animals living permanently on the marsh.

In the first group come sheep, rabbits, rats and mice, and a large number of birds. Since most of the birds come to feed on the animal life of the marsh their importance in the economy of the area is great, especially in times of drought when the water in the pools is shallow or has even disappeared. At such times the mud shows the tracks of innumerable waders which have crossed the mud in all directions in their search for the small crustacea, insect larvæ and worms which form their food. The numbers of these destroyed during the summer must be enormous in a secluded place, but at Aberlady a main road runs along the side of the marsh, and the activities of many of the shier birds are limited to the early hours of the morning.

In the second group are animals living on the surface of the marsh. This region is of interest from the point of view of respiration rather than from that of adaptation to changing salinity. Most of the species inhabiting it belong to the class Insecta, and, owing to their chitinous covering they are probably unaffected by saline conditions acting during short periods of time. On the other hand, they are all air breathers, and are cut off from their source of supply every time the marsh is covered by the tide. It is possible, however, that sufficient air is retained in their tracheæ to keep them alive in an inactive state until the water again recedes, or that they breathe anærobically during the short period. Slater (1930) has shown that it is possible for the Cockroach to remain in an oxygen-free atmosphere for as long as two hours without being permanently affected. It is seldom that any of the marsh is covered for as long a period.

At high-water mark a thick layer of weed, dead leaves, bits of wood and rubbish of all sorts, accumulates, forming a moist, warm region with a plentiful food supply. These conditions are taken advantage of by a number of animals, mostly Crustacea and Coleoptera. On the right bank the following species occur.

- Annelida.
  - *Enchytraeus albidus.*
- Crustacea.
  - *Orchestia gammarella.*
  - *Porcellio scaber.*
  - *Philoscia muscorum.*
- Myriopoda.
  - *Cylindroiulus britannicus.*
  - *Brachyiulus pusillus.*
  - *Polydesmis* sp.
- Insecta.
  - *Campodea palustris.*
  - Anthomyid larvæ.
  - *Tachinus rufipes.*
  - *Quedius maurorufus.*
  - *Lestiva longelytrata.*
  - *Pterotrichus diligens.*
  - *Dichirotrichus pubescens.*
- Arachnida.
  - *Lycosa palustris.*

On the left bank the drift is not so dense, and is deposited on long stiff grass so that the region is never so moist as on the right bank. The following species are found.

- Crustacea.
  - *Orchestia gammarella.*
  - *Porcellio scaber.*
- Myriopoda.
  - *Brachyiulus pusillus.*
- Insecta.
  - *Campodea palustris.*

On the right bank, where most of the soil is sandy, the surface of the marsh is dry, and the following species occur.

- Crustacea.
  - *Orchestia gammarella.*
- Insecta.
  - *Podura marina.*
  - *Campodea palustris.*
  - *Tachyporus hypnorum.*
  - *Atheta triangulum.*
  - *Atheta vestita.*
  - *Cantharus rusticus.*
  - *Dichirotrichus pubescens.*
- Arachnida.
  - *Lycosa palustris.*

On the left bank this type of surface is not represented.

Wherever mud accumulates the ground becomes wet and waterlogged. On this type of surface on the right bank the following species are found.

- Crustacea.
  - *Sphæroma rugicauda.*
  - *Orchestia gammarella.*
  - *Carcinus maenas.*
- Mollusca.
  - *Hydrobia ulvæ.*
  - *Littorina saxatilis.*
- Insecta.
  - *Podura marina.*
  - *Campodea palustris.*
  - *Tachyporus hypnorum.*
  - *Atheta triangulum.*
  - *Atheta vestita.*
  - *Dichirotrichus pubescens.*
- Arachnida.
  - *Lycosa palustris.*

Along the edge of the marsh, in crevices in the muddy bank and round the edges of the lowest pools, three other species occur: a small reddish turbellarian *Uteroporus vulgaris*, and an isopod, *Paragnathia maxillaris*, are numerous, but the third species, the mollusc, *Phytia myosotis*, is rare. Since it occurs commonly at the Tynninghame marsh near Dunbar, a search was made at Aberlady, and one large specimen and two small ones were obtained from among the grass roots.

On the left bank the ground is so wet that only the following species can live there.

- Annelida.
  - *Enchytræus albidus.*
- Crustacea.
  - *Orchestia gammarella.*
  - *Sphæroma rugicauda.*
  - *Carcinus maenas.*
- Mollusca.
  - *Hydrobia ulvæ.*
- Insecta.
  - *Podura marina.*
  - *Campodea palustris.*
  - *Dichirotrichus pubescens.*
- Arachnida.
  - *Lycosa palustris.*

The surface fauna of the marsh is derived from three sources. Species such as *Dichirotrichus pubescens*, *Atheta vestita*, *Orchestia gammarella*, *Phytia myosotis* and *Podura marina* occur only in regions within reach of the tide, and are found commonly on salt-marshes. Other species such as *Porcellio scaber* and *Philoscia muscorum*, *Atheta triangulum*, *Campodea palustris* and *Lycosa palustris* are commonly found away from the coast, but are not inconvenienced by a certain amount of salt water. Others such as *Hydrobia ulvæ*, *Sphæroma rugicauda*, *Carcinus maenas* and *Littorina saxatilis* are brackish-water or marine species which have been washed on to the marsh from the estuary, and which are able to survive in the moister parts in crevices and under banks.

THE FAUNA OF THE POOLS.

The pools on the marsh can be roughly divided into two groups: those which are situated near the top of the marsh, and are seldom reached by the tides, and those which are entered by many tides.

The less saline pools.

During the greater part of the year the first type of pool is almost fresh having a salinity of about $1{\cdot}0\,^{\circ}/_{\circ\circ}$. Immediately after a spring tide, however, the salinity may be as high as $15{\cdot}0\,^{\circ}/_{\circ\circ}$. It falls rapidly under normal circumstances, and in a week or two it has reached its ordinary low value (Fig. 14, p. 245). These pools contain little vegetation; a few are filled with *Scirpus lacustris* var. *tabernæmontani*, a few with *Zannichellia palustris* and *Equisetum limosum*, but the greater number are devoid of plant life except for a few diatoms and green flagellates. The bottoms of the pools are of soft mud mixed with dead leaves, overlying sand on the right bank and stiff clay on the left. The permanent fauna of these pools is limited to a few species, some of which may be found in neighbouring ponds, others are definitely brackish-water animals which are able to live in low-average salinities.

Fresh water species.

Insecta.
- *Cricotopus vitripennis.*
- *Culicella* sp.
- *Agabus bipustulatus.*
- *Hydroporus planus.*
- *Hydroporus palustris.*
- *Hydroporus nigrita.*
- *Hygrotus inæqualis.*
- *Helophorus viridicollis.*

Brackish water species.

Crustacea.
- *Gammarus duebeni.*
- *Tachedius brevirostris.*
- *Cyclopina gracilis.*
- *Eurytemora velox.*

Insecta.
- *Aëdes detritus.*
- *Ochthebius marinus.*

In addition to these animals which live and breed in the pools, others derived from the same sources are accidental visitors, which only find a temporary footing in the marsh when the conditions are suitable, and disappear again when these conditions change.

Fresh water species.

Mollusca.
    Limnæa truncatula.
Insecta.
    Sigara sahlbergi.
    Anopheles bifurcatus.
    Culex pipiens.
    Chloeon sp.
Amphibia.
    Molge palmata.
    Bufo vulgaris (tadpoles).

Brackish water species.

Annelida.
    Nereis diversicolor.
Crustacea.
    Sphæroma rugicauda.
    Corophium volutator.

The more saline pools.

The remainder of the pools on the marsh must be considered under one head from the point of view of salinity. Owing to their small size they are so greatly influenced by factors such as the rainfall, the rate of evaporation and the amount of drainage water entering them that they cannot be further subdivided on a salinity basis. The fauna of the pools, however, is by no means uniform, but differences in it can best be correlated with differences in the amount of vegetation and in the consistency and nature of the substratum rather than with arbitrary differences in the salinity.

Many of the pools contain an abundant supply of weed which in some consists of a luxuriant growth of *Ulva lactuca*, *Enteromorpha intestinalis*, *E. compressa* and *Polysiphonia elongata*, growing on the grass roots which form an overhanging mat round the margin. The bottoms of such pools may consist of bare mud covered at certain times of the year by a brown scum of diatoms. Other pools have a dense bottom vegetation as well as the fringing weed. In some this consists of *Zostera marina* (in one pool of *Z. nana* which was, however, killed off by the hot summer of 1932, and has not yet recolonised the marsh, although it is common on the muddy banks of the river), in other pools dense mats of species of Chætomorpha cover the bottom, and in others *Vaucheria littorea* fills the pools. In some, where solid objects such as stones, old tin cans or waterlogged wood occur on the substratum, *Enteromorpha intestinalis* and *Ulva lactuca* grow thickly. By far the most luxuriant of the algæ, however, is the Vaucheria which entirely covers the bottoms of many of the pools in the early spring and largely dies down by the end of May. In all pools where the substratum is exposed to light, in the spring and early summer a dense brown felt of diatoms is formed, and at the same season the fronds of the Zostera and the grass roots are covered with gelatinous masses of diatoms.

The nature of the substratum in the pools varies considerably. In a few, the bottom is covered with coarse gravel and stones ; in some it is sandy, particularly on the right bank of the burn, but in the majority it is covered to a depth of eight or nine inches with soft black mud, the surface inch of which is in a semiliquid state, becoming progressively firmer as greater depths are reached. The consistency of the mud is of great importance to some of the animals living in the pools and depends on the relative proportions of sand and silt, all grades between hard sand and almost liquid mud being represented. Since these differences are probably much more important than the exact salinity in determining the distribution of the fauna in a marsh such as this, the habitat has been divided according to the vegetation and to the nature of the bottom, and the associated faunas are listed separately.

The free swimming fauna.

A few free swimming forms occur which are independent of either the nature of the bottom or the kind of vegetation.

Brackish water species.

- Rotifera.
  - *Brachionus mulleri.*
- Crustacea.
  - *Neomysis vulgaris.*
- Insecta.
  - *Aëdes detritus.*
- Pisces.
  - *Gasterosteus aculeatus.*

Fresh water species.

- Rotifera.
  - *Notholca acuminata.*
- Crustacea.
  - *Eurytemora velox.*
  - *Tachedius brevirostris.*
  - *Cyclopina gracilis.*

In addition to these, adult specimens of *Aurelia aurita*, *Pleurobrachia pileus* and *Beröe cucumis* are occasionally carried into the pools by the tide and survive for a short time.

The fauna of the weed.

The following species occur on the vegetation fringing the edges of the pools.

Brackish water species.

- Cœlenterata.
  - *Syncoryne sarsi.*
- Crustacea.
  - *Sphæroma rugicauda.*
- Mollusca.
  - *Limopontia capitata* (small).
  - *Embletonia pallida.*
  - *Hydrobia ulvæ.*

Marine species.

- Annelida.
  - *Dinophilus tæniatus.*
- Nemertina.
  - *Lineus gesserensis.*
- Crustacea.
  - *Carcinus maenas* (small).

In addition to these species the following occur among the bottom vegetation.

Brackish water species.
Protozoa.
Pulvinula repanda.
Crustacea.
Jœra marina.
Melita palmata.
Gammarus duebeni.
Mollusca.
Alderia modesta.
Limopontia capitata.

Marine species.
Protozoa.
Polystomella striatopunctata.
Annelida.
Eulalia viridis.
Mollusca.
Mytilus edulis.

Fresh water species.
Insecta.
Chironomus aprilinus.
Procladius choreus.
Trichopteran larvæ.

Most of these are not confined to any one species of weed, but *Melita palmata*, *Alderia modesta* and *Limopontia capitata* when full grown are seldom found except on Vaucheria.

The fauna living on the substratum.

The following species occur in pools with stony bottoms.

Brackish water species.
Crustacea.
Gammarus duebeni.
Jaera marina.

Marine species.
Cœlenterata.
Aurelia aurita polyps.
Crustacea.
Balanus balanoides.
Mollusca.
Chiton marginatus.
Mytilus edulis.
Littorina saxatilis.
Littorina littorea.

None of the marine species are at all common, but they appear to be maintaining a precarious footing in a few of the pools.

The following species occur in pools with sandy bottoms.

Brackish water species.
Mollusca.
Hydrobia ulvæ.
Pisces.
Gobius microps.

Marine species.
Crustacea.
Carcinus maenas.
Crangon vulgaris.
Mollusca.
Littorina littorea.
Littorina saxatilis.

The following species occur in pools with muddy bottoms.

Brackish water species.
- Cœlenterata.
  - *Protohydra leuckarti.*
- Pisces.
  - *Gobius microps.*

Marine species.
- Crustacea.
  - *Crangon vulgaris.*

In the two last types of pool the following Protozoa are found on the surface of the substratum. *Chlamydodon triquetra*, *Euplotes charon*, *Loxophyllum rostatum*, *Lacrimaria olor*, *Uronychia transfuga*, *Pulvinula repanda* and *Polystomella striatopunctata* besides many other smaller species which have not been identified.

Pandalus annulicornis and *Pleuronectes flesus* also occur as occasional visitors.

The fauna living in the substratum.

The following species are found buried in the floor of pools with sandy bottoms.

Brackish water species.
- Annelida.
  - *Nereis diversicolor.*
  - *Manyunkia estuarina.*
- Crustacea.
  - *Corophium volutator.*

Marine species.
- Annelida.
  - *Arenicola marina.*
  - *Pygospio elegans.*
- Mollusca.
  - *Macoma balthica.*
  - *Mya arenaria.*

Fresh water species.
- Insecta.
  - *Chironomus aprilinus.*

The following species are found burrowing in mud.

Brackish water species.
- Annelida.
  - *Nereis diversicolor.*
  - *Manyunkia estuarina.*

Marine species.
- Annelida.
  - *Arenicola marina.*
- Crustacea.
  - *Carcinus maenas.*
- Nemertina.
  - *Lineus gesserensis.*
- Pisces.
  - *Anguilla vulgaris.*

Fresh water species.
- Insecta.
  - *Chironomus aprilinus.*

It is impossible to distinguish exactly between these two types of bottom, and only the fauna of the two extremes is given. Even so a considerable number of species occur in both.

THE FAUNA OF THE ESTUARY.

The estuary in the immediate vicinity of the marsh (Fig. 2) can be divided into four regions each showing slight differences in the fauna.

The mud. This region is best developed on the banks of the Peffer burn east of the foot bridge. The mud is soft and sticky and has a thick covering of *Zostera nana.* The following species are found.

- Annelida.
  - *Nereis diversicolor.*
- Crustacea.
  - *Corophium volutator.*
- Mollusca.
  - *Macoma balthica.*
  - *Scrobicularia piperata.*
  - *Hydrobia ulvæ.*

A similar fauna is found in the mud along the left bank of the burn near the hulks.

The sand. This region lies on the right bank of the burn west of the foot bridge. The following species occur.

- Annelida.
  - *Arenicola marina.*
  - *Nereis diversicolor.*
- Nemertina.
  - *Tetrastemma melanocephala.*
- Mollusca.
  - *Hydrobia ulvæ.*
  - *Cardium edule.*

Tetrastemma is not common and is found only under a few stones, although large numbers are present nearer the sea.

The stony mud. This region lies on the left bank between the marsh and the pure mud edging the bed of the burn at low water. It consists of gravelly mud on which rest stones of various sizes. The following species occur.

- Annelida.
  - *Nereis diversicolor.*
- Nemertina.
  - *Lineus gesserensis.*
- Crustacea.
  - *Balanus balanoides.*
  - *Corophium volutator.*
- Mollusca.
  - *Chiton marginatus.*
  - *Mytilus edule.*
  - *Littorina littorea.*
  - *Littorina saxatilis.*
  - *Hydrobia ulvæ.*

The bed of the burn at low water. This region always has running water varying in salinity from 0·8°/$_{oo}$ when the tide is out, to 33·0 to 35·0°/$_{oo}$ when the tide is full. A number of large stones lie in the stream which afford protection to the Mysids from the current. The following species are found.

- Crustacea.
  - *Corophium volutator.*
  - *Sphæroma rugicauda.*
  - *Gammarus duebeni.*
  - *Hyale nilsoni.*
  - *Neomysis vulgaris.*
  - *Crangon vulgaris.*
- Mollusca.
  - *Hydrobia ulvæ.*
  - *Littorina littorea.*
  - *Littorina saxatilis.*
- Pisces.
  - *Gasterosteus aculeatus.*
  - *Pleuronectes flesus.*
  - *Gobius microps.*

Although most of the species occurring in the estuary are the same as those found in the marsh, the following were found in the estuary only, *Scrobicularia piperata*, *Cardium edule*, *Hyale nilsoni* and *Tetrastemma melanocephala*.

NUMBERS OF ANIMALS IN THE MARSH.

The number of animals in the marsh is difficult to estimate, but is in some instances very large. For example, in one pool in June in an area of one square foot of mud there were 8890 young Nereis. Counts of the three principal inhabitants of the mud, *Corophium volutator*, *Chironomus aprilinus* and *Nereis diversicolor*, gave the following figures. These are for an area of one square foot and are the averages of five samples made at different times throughout the year.

TABLE I.

Species.	Pool II.	Pool III.	Pool VII.	Pool IX.	Pool XI.
Corophium volutator	64	84	36	108	15
Chironomus aprilinus	519	1239	1	66	81
Nereis diversicolor	36	3	9	48	60

Estimates of the numbers of the larger animals in some of the pools were also made, partly by sampling, partly by actual counts of random areas. The results are given in the following table.

TABLE II.

Species.	Pool VIII.	Pool IX.	Pool XI.	Pool XII.
Limopontia capitata	22	0	0	0
Hydrobia ulvæ	46	0	108	0
Mya arenaria	0	(41)*	(2)	0
Nereis diversicolor	3	10	6	0
Arenicola marina	4	(10)	(4)	0
Corophium volutator	0	3	34	322
Chironomus aprilinus	3672	572	8	78
Gobius microps	0	(3)	(1)	0

NOTES ON THE FAUNA.

Protohydra leuckarti. Protohydra is common at certain times in some of the pools. During May and June, 1931, it was present in large numbers in Pool VII. It was still abundant in October, but died out during the winter, and was not rediscovered until the summer of 1933, when it reappeared in Pool IV. The uneven distribution and the difficulty of seeing the animal probably accounts for the few records of its occurrence in Britain. Up to the present it has been recorded by Hickson only from Southampton and Plymouth, but a search in a small marsh at Torridon in Western Ross-shire revealed large numbers, again in one pool only, so that it is probably widely distributed.

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* The figures in brackets are for the whole pool, not per square foot.

Arenicola marina. The castings of this worm are to be found in pools of an average salinity as low as $15^{\circ}/_{oo}$. In these pools the salinity does not often fall below $8^{\circ}/_{oo}$. The nature of the bottom does not appear to affect the distribution, except that the worms do not occur in pools with gravelly bottoms. They are numerous in only a few pools, the maximum number recorded being 61 individuals of all sizes per square yard, the average number being 4 or 5.

The Copepods. The three species of Copepod which have been identified are most abundant in the fresher pools, although they also occur in some of the salter ones. In addition several species of Harpacticids are common in the fresher water, while a minute bottom living species is abundant in the surface layer of the mud of most of the salter pools.

Corophium volutator. The distribution of Corophium is determined firstly by the salinity, secondly by the type of bottom. In the upper pools of a salinity of about $5^{\circ}/_{oo}$ it only occurs as an occasional visitor. Hart (1930) states that Corophium when full grown is able to withstand immersion in fresh water for 16 days, but that the young die at the first moult. Only adults have been seen in the fresher pools. In the salter pools the distribution of Corophium is dependent on the type of bottom as Hart points out, being most abundant in muddy pools without vegetation. In one such pool the total number of animals per square foot was 322, exclusive of most of the smaller individuals which passed through the wire sieve. In sandier pools the numbers are low, for example, 34 per square foot, and in pools with black mud they may be absent.

Paragnathia maxillaris. This species occurs in burrows probably made by Orchestia, on the seaward edge of the marsh, above the bridge on the right bank only. The females are distended with fluid of a yellow colour. The young are found attached to Gasterosteus in the estuary, as many as seven being found on one fish.

Gammarus duebeni. This species is most abundant in the fresher pools round Pool XIII, on the right bank, and in the fresh water drains which traverse the marsh. It is sparingly distributed over the rest of the marsh but is common in the estuary. It breeds all the year round.

Neomysis vulgaris. This Mysid is common in the estuary as far up as the bridge but is local in its distribution in the marsh. In June, 1931, it was present in Pools III and VI only, but by September had spread to the surrounding pools. In 1932 specimens could be taken from many parts of the marsh but it appeared to be breeding only in a few pools.

After the hot summer it disappeared from all except Pool III, and from there died out during the winter. Since then it has not reappeared in the marsh although it is present in large numbers in the estuary. This may be due to the relatively low rainfall since the summer of 1932, causing much higher salinities in the pools. In the estuary, on the other hand, the Mysids are still subjected to almost fresh water conditions for the greater part of the twenty-four hours.

Carcinus maenas. Small specimens up to half an inch carapace width are common among the weed in the pools and also under dry overhanging banks on the marsh. They appear to be resistant to drought over long periods of time. Larger specimens are, however, present in considerable numbers in burrows from three to nine inches long under the overhanging banks of the pools and in the soft bottom mud. When the pools dry up they may be dug out, but are otherwise seldom seen as they emerge from their burrows only during the night.

Aëdes detritus. This mosquito is stated by Marshall (1925) to occur in stagnant full strength sea water as well as in brackish water. In the marsh, however, the larvæ are found only in pools of low average salinity. Since the eggs are scattered indiscriminately over the surface of the marsh and only hatch in suitable situations, one might expect to find a certain number of larvæ in all the pools. Gasterosteus and Gobius eat them however with avidity and probably clear any pool of the early stages, so that the larvæ should only be found in the upper pools where fish are absent. This cannot be the only controlling factor since fish are absent from many of the lower pools, yet Aëdes is never found in them.

Chironomus aprilinus. The larvæ of this species do not appear to be affected by the salinity since they occur in all pools, provided that the substratum is sufficiently soft. In some pools enormous numbers are present; 3660 per square foot were counted in Pool VIII. In others, such as Pool XI, which is sandy, only 10–20 per square foot may be present.

Culex pipiens. Although this species occurs with *Culicella morsitans* and *Anopheles bifurcatus* in the neighbouring ponds, it has been found only once in the marsh pools. In June, 1931, it occurred in enormous numbers in Pool X. The salinity at the time was between 1·3 and 0·9$^{\circ}/_{\circ\circ}$, but, although as low salinities are common in certain pools, the larvæ have never again been found in the marsh.

Alderia modesta. This nudibranch occurs in large numbers among the Vaucheria in the pools. It arrives in the marsh at the same time as Limopontia and behaves in the same way.

Limopontia capitata. This small nudibranch is of considerable interest. Although reported occasionally from rock pools near high-water mark, its most characteristic habitat is the pools of salt-marshes, but its appearance there is seasonal. The molluscs were first observed at Aberlady in June, 1931, but had entirely disappeared by October. In 1932 and 1933 they appeared after a high tide in the middle of February. Breeding began almost at once and spawn was found as late as June. Small Limopontias were found from March onwards in the weed fringing the pools, while the adults were entirely confined to *Vaucheria littorea*, or to the pools where it had been. During the winter of 1933–34 the characteristic egg masses of Alderia were observed in a pool at the end of November and a search revealed immature Limopontias also. They quickly increased in size and began to spawn in January. This early arrival in the marsh may have been due to the hot summer and the exceptionally open winter. The complete life-history of these molluscs is not known. The eggs hatch as veligers, but the later stages have never been seen in the pools, neither are their winter quarters known nor their method of arrival in the pools.

Hydrobia ulvæ. This species occurs in the pools with a firm substratum and along the banks of the stream. In pools where the mud is in a semi-liquid condition a few specimens may be found, but unless weed is present on which the animals can crawl, they are not abundant. Robson (1920) showed that in an Essex marsh the numbers of *Hydrobia ulvæ* were controlled by the distribution of *Ulva lactuca* on which, he says, they were feeding. This association is by no means universal. At Aberlady the Ulva is remarkably free from Hydrobia which occurs much more frequently among Enteromorpha. The greatest numbers, however, are to be found in the sandy pools on the right bank which dry up completely between tides. Counts were made in a number of these pools and 360 to 590 individuals per square foot were often found. In selected parts the population was as high as 2570 per square foot. Above the bridge on the bare mud of the right bank 3020 animals per square foot were present and on the clean sand below the bridge 830. In all these places *Ulva lactuca* was completely absent. Specimens of an average length of 9 mm. have been taken from the muddy flats of a salt marsh at Tynninghame in East Lothian, and from the sand at the head of some of the long inlets on the west coast of the Outer Hebrides, where there is no Ulva. An examination of the stomach contents shows that Hydrobia is a detritus feeder. It is likely that its occurrence on Ulva in the Essex marsh was connected with the soft nature of the substratum and not with the food supply.

Mya arenaria. Mya occurs in the marsh particularly in Pools III, IX, and XI. The first of these has a sandy bottom while the others have soft mud. The salinity in all three is usually high. During the summer of 1933 a Mya in a pool with a muddy bottom which had dried up was kept under observation. After five weeks of drought the animal was still alive. By the end of the summer, however, it had died. During 1934, when Pool XI was dry for many periods during the summer, nearly all the Mya were killed, but those in Pools III and IX did not suffer although the salinity rose considerably above that of the outside sea water. These pools never dried up.

Gasterosteus aculeatus. These fish are evenly distributed throughout all the salter pools in the marsh between the end of February and the end of August. The nests are made of weed and placed in the open on the mud. In contrast to the early arrival of the nudibranchs, the first sticklebacks were not seen in 1934 until the beginning of April, and the main body arrived still later. The adults and young are often almost entirely killed off by the drying up of the pools during the summer. This occurred in 1933 and as a consequence the fish were present in smaller numbers in 1934.

Gobius microps. The adults and young of these small fish inhabit the pools all the year round. They spawn during the month of June, attaching the eggs to the under sides of shells, bits of paper or dead leaves, the fish congregating in numbers round suitable objects.

Bufo vulgaris. Although toads breed freely in the fresh water ponds at Aberlady and are known to be tolerant of a certain amount of salt, eggs and larvæ have been seen in only one pool, the salinity at the time being $0{\cdot}2^{\circ}/_{oo}$. In other marshes they have been found in a salinity of at least $4{\cdot}8^{\circ}/_{oo}$.

Molge palmata. A single specimen of this newt was taken in Pool XIII in the spring of 1934. The salinity at the time was $0{\cdot}8^{\circ}/_{oo}$. Earlier in the spring, when salinities were higher, dead specimens of *Rana temporaria* were common in the pools in this region.

THE ENVIRONMENT.

The Salinity.

i. *The conditions in the pools.*

The salinity of the pools is influenced by four main factors.

(1) Tides.
(2) Rainfall.
(3) Evaporation.
(4) Interchange of water between the mud and the overlying water of the pool.

The effect of the first and the last of these factors depends on the previous history of the pool under consideration; for instance, a tide entering a pool after a period of wet weather raises the salinity, a tide entering the same pool after prolonged drought lowers it.

The Tides.

Only a certain number of tides in the year affect the conditions in the marsh, since the water must rise at least sixteen feet above datum before it enters any of the pools. Thus the maximum numbers of tides entering the lowest pool on the marsh would be, according to the Admiralty Tide Table, twenty-five per year, that is, at every new and full moon. Pools situated at the top of the marsh are, of course, reached by fewer tides. The wind may cause an appreciable variation in these conditions. A strong offshore wind coinciding with a poor tide may prevent sea-water reaching some of the pools. Conversely, under the influence of an onshore wind, the sea water may enter pools on the marsh which it would not normally have reached. The effect of an onshore wind is intensified by the funnel-like shape of Aberlady Bay. The number of tides entering a pool depends also on the height above datum of the lowest part of the rim of the pool and not on its position in the marsh, since the surface is by no means level and certain pools are raised many inches above their neighbours.

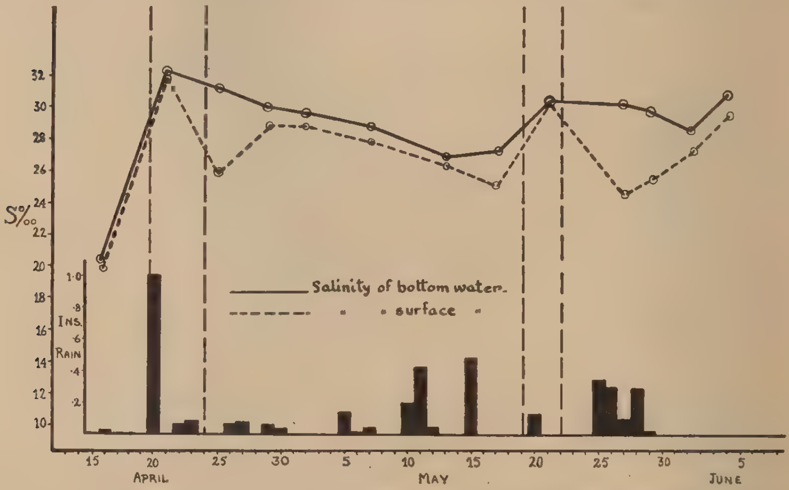


FIG. 3.—The salinity changes in Pool VII during the spring of 1932 showing the effect of tides entering the pool when the rainfall and the amount of evaporation have been approximately equal. The vertical lines show the limits of the periods during which tides entered the pool.

The effect of a tide entering a pool is determined by the previous weather conditions in the district. If, since the last high tides, the amount of rain and the amount of evaporation have been approximately equivalent, the passage of a tide over the marsh has little effect on the salinity of the water of the pools. Approximately these conditions are illustrated in Figure 3 for Pool VII during the period April 16th to June 4th, 1932. Tides entered the pool between April 20th and 24th and between May 19th and 22nd. In the intermediate period the rainfall was slightly greater than the evaporation and the salinity of the bottom water fell from 32·5 to

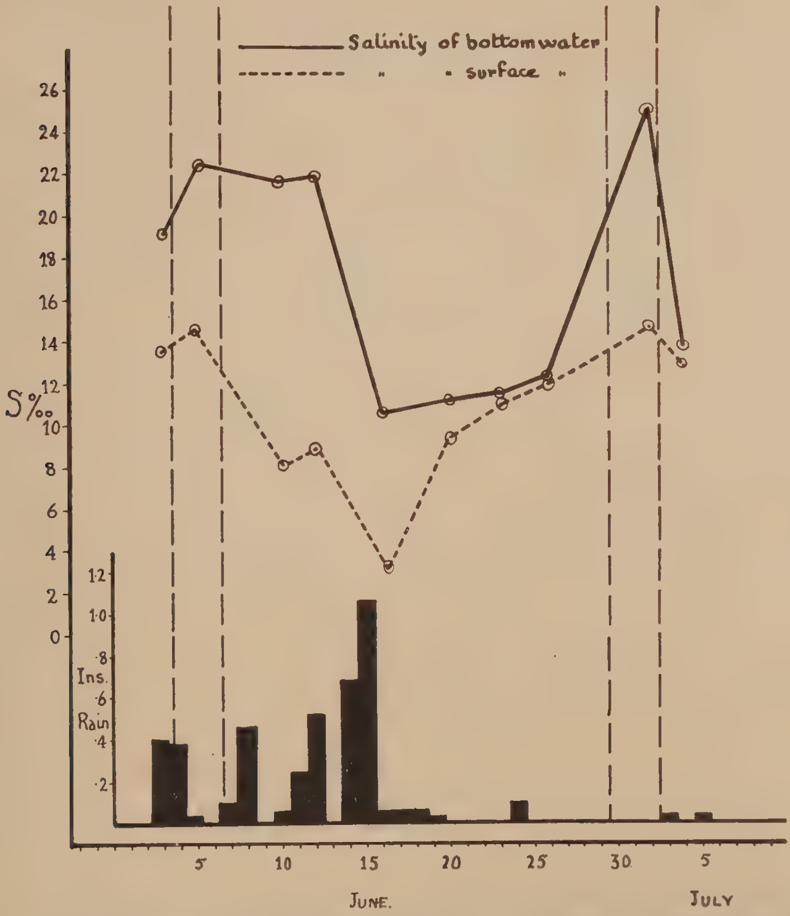


FIG. 4.—The salinity changes in Pool III during June, 1931, showing the effect of tides entering the pool when the rainfall has been greatly in excess of the evaporation. The vertical lines show the limits of the periods during which tides entered the pool.

$27{\cdot}0^{\circ}/_{\circ\circ}$. The surface water showed greater changes, falling from 32·0 to $25{\cdot}0^{\circ}/_{\circ\circ}$ following heavy rain. If these conditions are compared with those in Pool III during a period of very wet weather (Fig. 4) the comparative slightness of the salinity changes will be appreciated. If, since the last tides, the rainfall has greatly exceeded the evaporation, a tide covering the marsh raises the salinity of the water. This condition is shown in Figure 4 which illustrates the changes in Pool III during the period June 3rd to July 5th, 1931. Tides entered the pool on June 4th to 6th and from June 30th to July 2nd. The salinity of the surface and bottom water fell from 14·5 to 3·0°/$_{oo}$ and from 22·5 to 10·5°/$_{oo}$, changes three times as great as those illustrated in Figure 3. If, however, the rate of evaporation has exceeded the rainfall since the last tide, then water entering the pool lowers the salinity. This condition is illustrated in Figure 5 for Pool III during part of May and June, 1933, when the salinity of both surface and bottom water rose from 32·0°/$_{oo}$ on May 18th to 38·0 and 37·0°/$_{oo}$ respectively on June 20th. On June 24th and 25th tides just reached the pool, lowering the salinity to 33·5°/$_{oo}$.

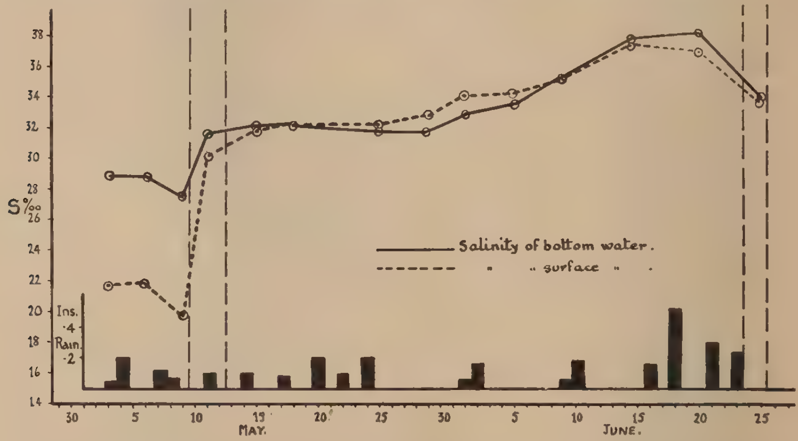


FIG. 5.—The salinity changes in Pool III during May and June, 1933, showing the effect of tides entering the pool when the evaporation has been in excess of the rainfall. Inverse layering of the water has taken place. The vertical lines show the limits of the periods during which tides entered the pool.

Rainfall.

The rainfall can influence the salinity of the pools in three ways: directly; by drainage into the pools from a higher level; or by flooding at the time of high tides.

The direct effect of rainfall is often well marked, as in Pool III (Fig. 4) during the month of June, 1931. The first half of the month was abnormally wet, with a total of 3·95 inches of rain in fifteen days. This rain, particularly that which fell on the 14th and 15th, is clearly reflected in the salinities of both the surface and bottom water, which fell from 14·5 to 3·0°/$_{oo}$ and from 22·5 to 10·5°/$_{oo}$ respectively. Vertical mixing of the water must have taken place here to a considerable extent for the bottom

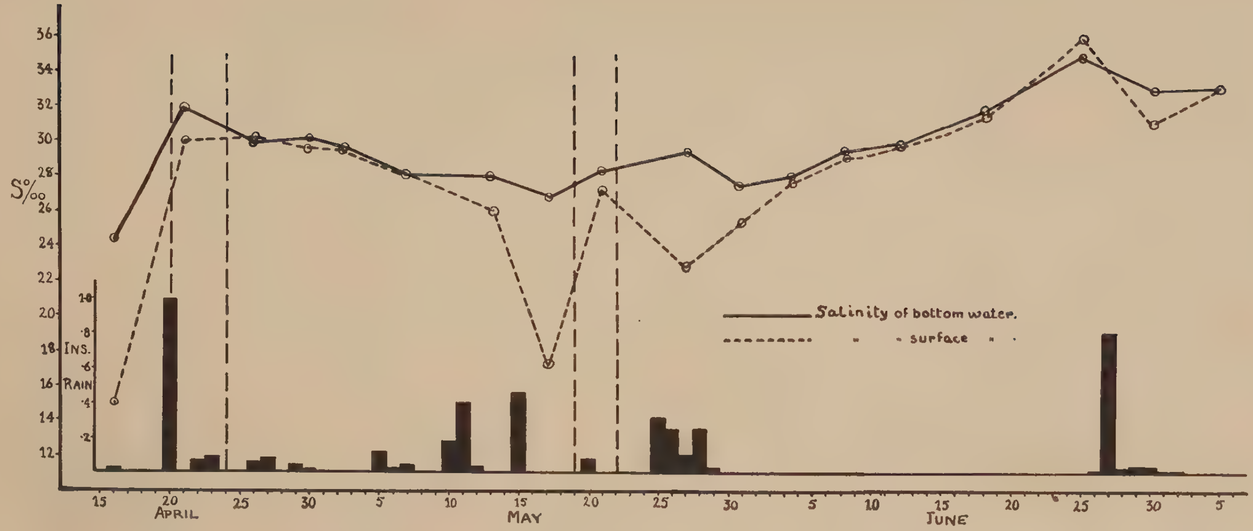


FIG. 6.—The salinity changes in Pool III during the spring of 1932 showing the lowering of the surface salinity by heavy rain and the effect of evaporation. The vertical lines show the limits of the periods during which tides entered the pool.

water to be so greatly affected. When there is no wind to bring this about the surface salinity is alone affected as in Figure 6, which shows the effect of rain unaccompanied by wind on the salinity of Pool III. Heavy rain between the 10th and 15th and the 25th and 28th of May lowered the surface salinity from 28·0 to 17·0 and from 27·0 to 23·0°/$_{oo}$ without appreciably affecting the salinity of the bottom water.

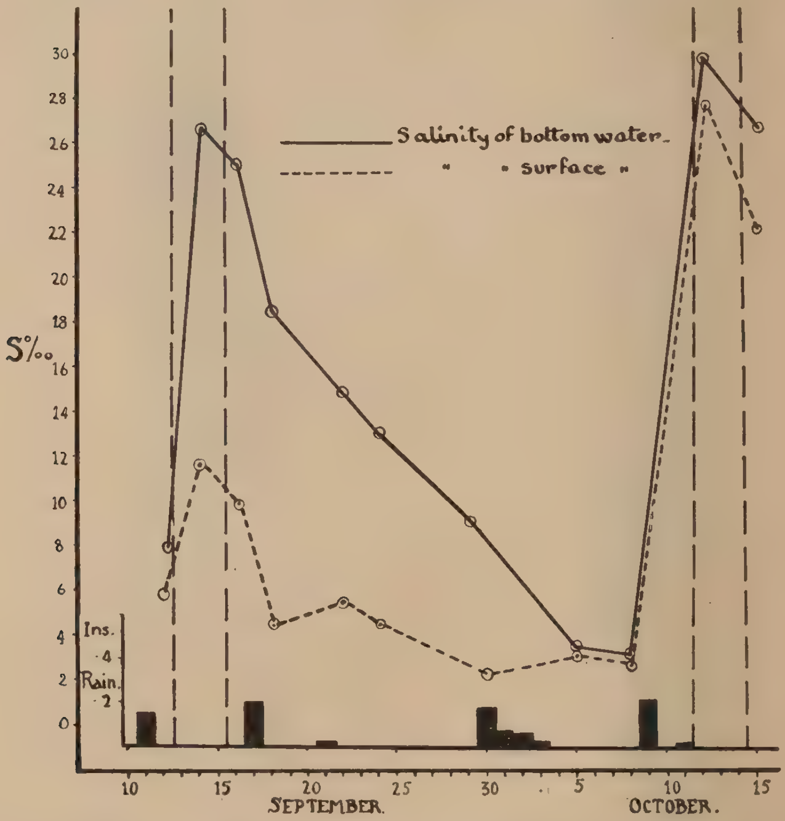


Fig. 7.—The salinity changes in Pool X during the autumn of 1931 showing the effect of drainage water. The vertical lines show the limits of the periods during which tides entered the pool.

The indirect effect of rainfall through drainage is well marked in certain pools near the top of the marsh, especially on the right bank, although it is often difficult to distinguish from that of direct rainfall accompanied by wind. When, however, a dry period follows rain, drainage into the pools from the land behind continues for some time, and the effect is easily seen as in Figure 7 for Pool X. The first fortnight of September, 1931, was fairly wet, 1·2 inches of rain falling in fifteen days, and tides entered the pool on September 13th to 15th, raising the salinity of the bottom water to 26·5 $^{\circ}/_{\circ\circ}$, but the surface water only to 11·5$^{\circ}/_{\circ\circ}$. After rain on the 17th the surface salinity fell to 4·5$^{\circ}/_{\circ\circ}$, and later to between 2 and 3$^{\circ}/_{\circ\circ}$. During the same period the salinity of the bottom water fell steadily until it became almost the same as that of the surface water. While mixing may have played some part, it is probable that drainage into the pool from the land behind was chiefly responsible for the large and steady decrease in salinity of the bottom water and the production of uniform conditions throughout. Confirmation of this is obtained from the changes in the alkali reserve. During the same period the alkali reserve of the bottom water rose steadily from 0·0022 N. to 0·0076 N., which would not have occurred had the fall in salinity been due to direct rainfall.

The rainfall also acts indirectly by affecting the salinity of the water entering the pools at each tide. Since Aberlady Bay drains dry at low tide, the water of the Peffer Burn does not accumulate in the bay but is carried out to sea and does not affect the salinity of the Forth appreciably. The data given in the Hydrographical Tables of the Conseil International pour L'Exploration de la Mer (1925–31) show that the salinity of the water at the mouth of the bay varies only slightly, the maximum values for the period 1925–31 at the surface and at 10 metres being 34·28 and 34·26$^{\circ}/_{\circ\circ}$ and the minimum 33·6 and 33·78$^{\circ}/_{\circ\circ}$ respectively. The effect of the incoming tide will be, however, to dam back the water of the burn in the region of the marsh, and this water, mixing to various extents with the sea-water, spreads over the marsh as the tide rises. The amount of water coming down the Peffer fluctuates considerably. The following rough estimates were made of the volume of water flowing per minute under varying weather conditions.

TABLE III

	Gallons.
October 24th, 1933, after a very dry summer	2,800
November 27th, 1933, after slight rain	3,100
April 14th, 1934, after 10 days' heavy rain (2·83 in.)	48,000
April 24th, 1934, after 10 days' dry weather (0·61 in.)	5,200
May 31st, 1934, after another 5 weeks' dry weather(1·51 in.)	2,700
June 14th, 1934, after another 2 weeks' drought (0·23 in.)	1,700

During wet weather then, large quantities of fresh water flow down the stream and are met by the incoming tide, a certain amount of mixing finally taking place. The effect of this is clearly shown in Figure 8, which gives the conditions in Pool XI in June, 1931, when the first half of the month was abnormally wet. Tides entered the pool during three periods, June 3rd to 6th, 17th to 20th, and June 29th to July 3rd. The first group of these tides only raised the salinity from 11·5 to 12·0°/$_{oo}$, owing to the large amount of flood water. On the 16th the rain practically ceased, although flood water was still coming down, for the second batch of tides raised the salinity of the top and bottom water of the pool only to 19·0 and 21·0°/$_{oo}$, and the third to 19·5 and 20·5°/$_{oo}$. Under ordinary weather conditions a spring tide would raise the salinity of this pool at least to 30°/$_{oo}$. In calm weather the water of the Peffer Burn does not mix completely with the water coming in from the sea, but flows out over the surface as a layer of almost fresh water. The following table gives the

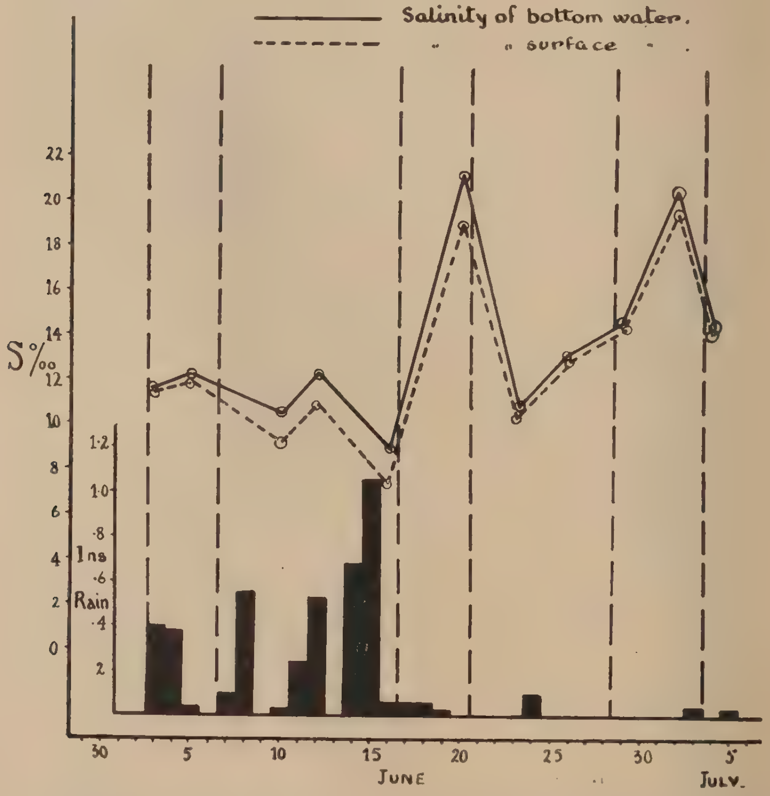


FIG. 8.—The salinity changes in Pool XI during June, 1931, showing the effect of the damming back of the flood water of the Peffer Burn by the incoming tide. The vertical lines show the limits of the periods during which the tides entered the pool.

salinity at the footbridge in the centre of the estuary, and at various depths under various weather conditions.

The first set of figures was obtained in June, 1933, when the river was low and the weather calm. The second set was obtained in April, 1934, on a calm day after ten days' heavy rain.

TABLE IV

Time.	Depth of sample.	Depth of water.	Salinity ‰.
12.15 p.m.	Surface	6 in.	1·0
	Bottom		1·0
12.45 p.m.	Surface	2 ft.	24·8
	1 ft. below		26·8
	Bottom		27·6
1.15 p.m.	Surface	3 ft. 4 in.	29·4
	1 ft. below		30·6
	Bottom		30·6
1.45 p.m.	Surface	5 ft. 9 in.	31·0
	1 ft. below		31·5
	4 ft. below		31·7
	Bottom		32·2
2.15 p.m.	Surface	5 ft.	29·8
	1 ft. below		29·8
	4 ft. below		29·9
	Bottom		29·9
High water 2.03 p.m.			
11.45 a.m.	Surface	1 ft.	0·8
	Bottom		0·8
12.30 p.m.	Surface	1 ft.	0·8
	Bottom		0·8
1.45 p.m.	Surface	2 ft. 8 in.	2·8
	1 ft. below		12·6
	Bottom		13·4
2.30 p.m.	Surface	4 ft. 6 in.	13·2
	1 ft. below		28·5
	Bottom		29·3
3.15 p.m.	Surface	6 ft. 3 in.	21·4
	1 ft. below		31·1
	4 ft. below		32·0
	Bottom		32·6
High water 3.15 p.m.			

The effect of this layering of the estuarine water can be seen in the salinity curves for various pools. In Figure 7 the condition is particularly well shown for Pool X during part of September and October, 1931. The first half of September was wet, 1·2 inches of rain falling, and a considerable amount of water was flowing in the Peffer. On September 13th a tide entered the pool and must have raised the salinity to at least 26·5$^{\circ}/_{\circ\circ}$. On the following day, which was windless, the tide just reached the pool by creeping between the grass stems. Water samples taken immediately after the tide receded showed that although the salinity of the bottom water was as high as 26·5$^{\circ}/_{\circ\circ}$ the surface water was only 11·5$^{\circ}/_{\circ\circ}$. Water samples taken in the estuary at high tide showed that there was a marked difference between the salinities of the surface and bottom water, the value for the former being 5·5 and for the latter 31·3 $^{\circ}/_{\circ\circ}$; so that the water reaching Pool X must have been surface water of low salinity, thus giving the low value for the surface water of the pool. A similar discrepancy between top and bottom water is well marked in Figure 4 for Pool III at both periods of high tides.

Layering of the water. During periods of dry weather following a high tide the salinity of the water may be the same throughout. Such a condition is well shown in Figure 6, giving the salinities in Pool III, where, on June 4th, the salinity of the surface and bottom water was almost the same, and remained so during the next three weeks. If the pool is shallow, even during wet weather there may be little difference in the salinity at different depths. This is shown in Figure 8 for Pool XI where the maximum depth was five inches, and sufficient mixing took place to keep the salinity constant. Conditions of equal salinity are the exception, however, and there is often a marked difference between the surface and bottom layers. This difference may be due to two causes:

(*a*) Rain.
(*b*) Evaporation.

When heavy rain falls a layer of fresh water is formed on the surface of the pool, which during calm weather mixes slowly by diffusion. Figure 9*a* shows the conditions in Pool III. On October 20th, immediately after a high tide and before rain, the salinity was practically uniform throughout (Curve A). On the 22nd heavy rain fell, and on the 23rd the surface and bottom salinities were 17·6 and 31·2$^{\circ}/_{\circ\circ}$ respectively (Curve B). Between the 23rd and 26th it was windy and vertical mixing of the water took place, a condition of almost equal salinity being again achieved at about 26·5$^{\circ}/_{\circ\circ}$ (Curve C). If, on the other hand, the wind and the rain come together, then a definite layer of fresh water is not formed on top and mixing takes place rapidly until a uniform condition is again reached. This condition is shown in Figure 9*b*, for Pool V, where Curve A shows the condition of uniform salinity immediately after a high tide; Curve B, the condition two days later after wind and rain—mixing has already taken place to within two inches of the bottom; and Curve C, three days later, when the salinity has again become uniform throughout. The rainfall can also bring about layering of the water by means of drainage. This drainage water flows through the soil from the land behind the marsh, particularly in certain places, and reduces the salinity of the mud and overlying water. Figure 9 *c* shows the effect of drainage water on Pool XI. On October 26th (Curve A) conditions were fairly uniform. Rain accompanied by wind lowered the salinity of all the water to a certain extent (Curve B). The water at the surface of the mud, however, shows a markedly lower salinity than the water two inches above, which is probably due to drainage water. Inverse layering may also be produced if the weather is hot and dry.

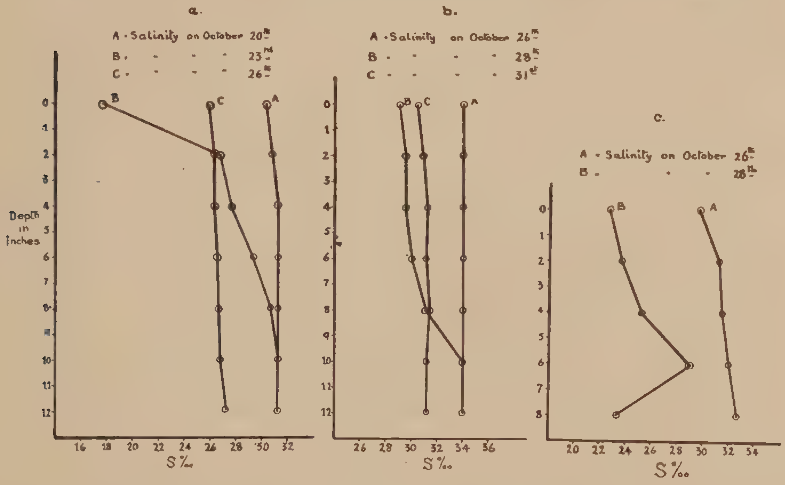


FIG. 9.—The salinity of certain pools at different depths to show (*a*) the effect of heavy rain in calm weather and the effect of wind in restoring conditions of equal salinity; (*b*) the effect of rain accompanied by wind; (*c*) the effect of drainage water.

Evaporation. Evaporation is always taking place from the surface of the pools, but its effect is usually so overlaid by other factors such as rainfall and the incidence of the tides that it is completely masked. During dry sunny weather, however, its results are well shown as, for instance, in Figure 6 for Pool III. The surface salinity first rose from 22·8 to 27·8°/$_{oo}$ on June 4th, then both surface and bottom salinity rose together to 36·0 and 35·0°/$_{oo}$ respectively on the 25th, after which rain fell. During the summer of 1933 the effect was even more pronounced, when, in spite of constant small amounts of rain, the salinity of Pool III rose from an average of 31·0$^{\circ}/_{\circ\circ}$ on May 11th to 37·5$^{\circ}/_{\circ\circ}$ on June 20th, after which a tide entered the pool and lowered the salinity (Fig. 5).

In warm, dry weather evaporation can proceed so rapidly that inverse layering takes place, the surface water being at a higher salinity than the water below. An example of this is shown also in Figure 5 for Pool III, where, from May 18th to June 9th, the salinity of the surface water was slightly higher than that of the bottom water. A certain amount of mixing, however, takes place all the time in the pools, and the difference can never be very great.

It is only during exceptionally hot, dry weather that the salinity in the pools rises above that of the Firth of Forth. This happened in the early summer of both 1932 and 1933. In the latter year the salinity rose as high as 38·2$^{\circ}/_{\circ\circ}$ on the 20th of June, after which the records had unfortunately to be discontinued.

Interchange between the mud and the overlying water. The effects of the interchange between the mud and the water cannot in most cases be estimated, since they are obscured by the effects of mixing, drainage and rain water. Under exceptional conditions, however, the rate of exchange can be observed. In October, 1933, Pool I was dry, but on the 23rd heavy rain fell, filling the pool to a depth of two inches. On the 24th the salinity of the bottom water was already 6·4$^{\circ}/_{\circ\circ}$ and of the surface water 5·8$^{\circ}/_{\circ\circ}$. On the 27th the bottom salinity had risen to 21·0$^{\circ}/_{\circ\circ}$, and the surface to 6·8$^{\circ}/_{\circ\circ}$. On the 30th rain fell and drainage water began to run in, lowering the salinity of both top and bottom water.

ii. *Conditions in the mud.*

Up to the present only the conditions in the water have been considered. However, since many salt-marsh animals inhabit the mud in the bottom of the pools, the conditions there are of equal importance. There seem to be two main factors involved :

(*a*) the salinity of the overlying water. .
(*b*) the amount of drainage water.

Under conditions of drought, however, a third factor, evaporation, comes into play ; after the overlying water of the pool has disappeared the heat of the sun and the wind act directly on the surface of the mud and profoundly alter the salinity.

The salinity of the overlying water. Table V gives the conditions in Pool XI, which can be taken as typical of the conditions in pools frequently entered by the tides.

TABLE V

SALINITY $^{\circ}/_{oo}$.

	April.				May.			
	19th.	22nd.	25th.	29th.	3rd.	6th.	9th.	11th.
Bottom water	24·8	20·8	18·4	17·4	14·2	12·8	30·6	32·0
Mud 0–1 in.	30·4	24·2	22·0	19·9	13·7	12·1	23·4	31·4
1–2 in.	24·3	25·0	22·9	18·3	16·7	15·9	17·2	23·5
2–3 in.	28·5	25·5	23·2	21·4	20·0	18·1	18·3	20·6
3–4 in.	27·6	26·1	25·5	21·9	21·7	19·4	21·3	19·3

	May.				June.			
	15th.	18th.	26th.	30th.	2nd.	6th.	9th.	13th.
Bottom water	27·6	26·4	19·6	18·6	17·6	16·0	31·2	30·6
Mud 0–1 in.	29·6	30·4	21·0	19·5	18·5	18·2	30·0	29·9
1–2 in.	28·7	26·3	22·4	18·8	17·7	16·8	24·8	29·0
2–3 in.	26·5	24·7	22·9	22·3	18·6	15·2	18·7	27·0
3–4 in.	23·6	20·8	21·6	23·2	20·1	18·8	25·0	26·6

Tides entered the pool on April 16th (the record commenced on the 19th), May 8th to 12th, and again on June 8th to 11th. The fluctuation in the salinity of the bottom water is considerable, and shows a maximum range of 19·2$^{\circ}/_{oo}$. The salinity of the surface inch of mud follows that of the water fairly closely, but shows a considerable lag in reaching its maximum and minimum values, and seldom reaches the same extremes of salinity. An exception to this occurred on May 6th, when the salinity of the mud actually fell below that of the water, possibly due to subterranean drainage water after fairly heavy rain on May 4th (for the rainfall record see Fig. 13). The maximum range is 19·3$^{\circ}/_{oo}$. The layer of mud 1–2 in. below the surface shows a similar lag, and the maxima and minima are less extreme, the total range being 13·1$^{\circ}/_{oo}$. In the deeper layers this is more and more marked, the range of salinity for the layer 2–3 in. below the surface being 11·9$^{\circ}/_{oo}$, and for that 3–4 in. down 8·8$^{\circ}/_{oo}$. At slightly greater depths it is reasonable to suppose that a condition of uniform and moderate salinity would be reached, at any rate, in pools with this type of bottom.

Drainage water. Drainage water can be of two kinds, fresh water coming from the land and salt water coming from the sea. It is impossible to say how far the second influences the condition in the marsh, but in certain regions there is a layer of coarse sand some inches below the surface, along which water appears to be pushed by the rising tide, altering the salinity of the mud in certain pools. In other regions the pools are unaffected by any tides except those reaching them in the normal manner. The effect of both kinds of drainage water is shown for Pool XIII during the spring of 1933 in Table VI.

TABLE VI.

Salinity $^{\circ}/_{\circ\circ}$.

	April.				May.			
	19th.	22nd.	25th.	29th.	3rd.	6th.	9th.	11th.
Bottom water	14·6	12·6	10·1	9·2	6·9	6·5	5·6	4·6
Mud 0–1 in.	11·9	12·3	8·2	6·5	6·0	5·6	3·9	5·9
1–2 in.	4·6	8·8	6·1	5·0	5·6	3·5	4·4	3·0
2–3 in.	2·2	2·6	2·8	3·4	3·5	2·4	5·1	6·0
3–4 in.	1·5	1·5	1·5	1·5	2·0	1·0	4·4	2·8

	May.				June.			
	15th.	18th.	26th.	30th.	2nd.	6th.	9th.	13th.
Bottom water	3·7	2·6	2·0	1·7	1·4	1·6	1·6	1·6
Mud 0–1 in.	4·9	4·5	2·3	1·7	1·7	2·0	1·0	1·0
1–2 in.	3·3	3·6	2·7	2·4	1·8	1·1	2·0	1·2
2–3 in.	2·3	2·2	2·5	1·8	2·8	2·2	2·2	1·5
3–4 in.	2·9	3·0	2·1	2·0	1·9	2·1	2·8	2·0

From April 19th till May 9th the salinity of the mud was lower than that of the bottom water, and, as the salinity of the latter fell under the influence of drainage water, that of the mud fell also. As the mud continued to have a lower salinity than the water it also was being affected by drainage water. On May 9th the salinity of the mud began to be considerably disturbed, rising and falling in an irregular manner for some days. This period of disturbance coincided with the high tides, which, forced in by a strong wind, covered the marsh to within about 20 feet of Pool XIII from the 9th to the 12th. It is probable that the salter water was forced up by the tide along the sandy layer under the pools which is present in this region, and caused the salinity changes in the mud. Similar though less well marked disturbances coincided with the next batch of high tides between June 9th and 12th, and confirmation of the results was obtained from other pools at the same time.

Evaporation. During the summer the tides may fail to reach the marsh pools for as long as six weeks, and if these periods coincide with periods of dry weather, then many of the pools dry up entirely, leaving the mud below directly exposed to the heat of the sun. The resulting changes vary with the type of bottom. In a pool floored with stiff mud the surface dries and cracks, and finally, if the drought is prolonged, the top inch of the mud cakes hard and can be lifted off. All animals living in this layer dry up unless they can burrow deeper into the mud. Small Corophium, Chironomus larvæ and young Nereis, as well as surface-crawling forms, are killed, but the layers below do not show an abnormal amount of drying or a very high chlorine content, so that deep-burrowing animals such as Mya, adult Nereis and Arenicola stand a good chance of surviving drought. Figure 10 shows the conditions in one such pool in the summer of 1932. Owing to the effects of drainage water the salinity of the water of the pool was low during the early part of May. On June 4th, just before drying up, the salinity of both top and bottom water was 10·5°/₀₀, or 5·8 gm. of chlorine per litre. At the same time, the values for the water contained in the mud were slightly higher, varying between 6·5 and 9·5 in the top four inches of mud. As soon as the pool dried up completely the surface layer of mud also began to dry and the chlorine content of the water to rise. By the 14th it had reached 22·0 gm. per litre, and by the 24th 60·0 gm. per litre. The layers below the surface inch of mud differed very little in their chlorine content. By the 14th they had risen to between 8·5 and 10·5, and by the 24th they had only risen to between 18·5 and 21·0 gm. of chlorine per litre, about one third of the value for the surface inch. A downpour of rain on the 25th caused a drop to 26·0 gm. per litre without appreciably altering the chlorine content of the layers below. By the 4th of July drainage had lowered the surface layer to 17·4, and the layers below to 12·0 gm. of chlorine per litre.

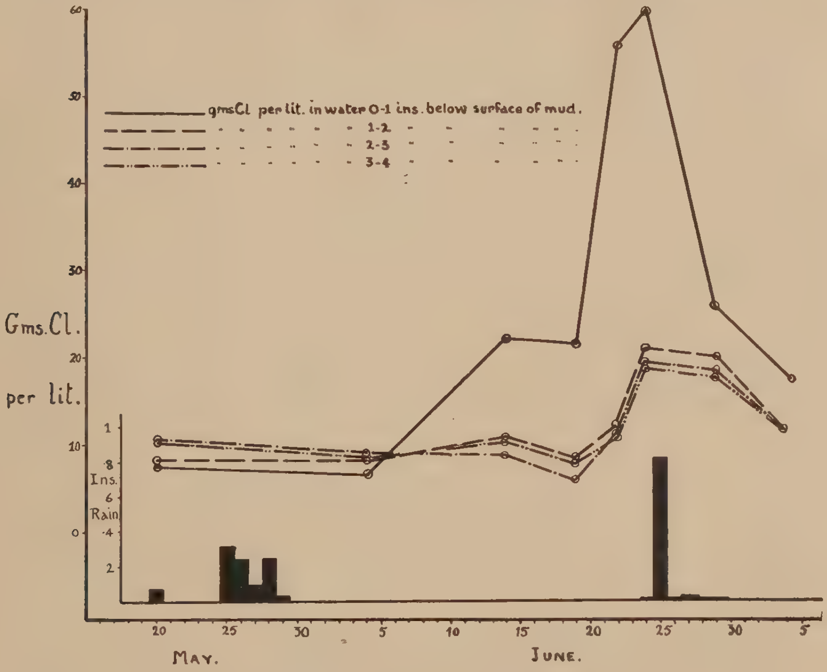


FIG. 10.—The changes in chlorine content of the water in the upper layers of the mud in Pool I during a period of prolonged drought.

As a contrast to the conditions in a muddy pool, the conditions in Pool XI can be taken. Here the bottom is sandy and when the pool is dry the top layer does not cake into a protective covering but remains free and porous. The result is that the layers below dry to a much greater extent than in a muddy pool. This particular pool contained a number of Mya and Macoma, which were all killed in 1933, when the pool was subjected to many recurring periods of dryness. The following table gives the values of the chlorine content of the water during one such period. It can be seen that although the surface inch gives some protection, there is not the marked difference between the layers that there is in Pool I with a muddy bottom. The drop in chlorine content on the 6th was due to a tide, which just reached the pool but did not leave any standing water.

TABLE VII

Depth.	Chlorine in gm. per litre.						
	May.			June.			
	18th.	26th.	30th.	2nd.	6th.	9th.	13th.
Bottom water . .	8·4	8·6	—	—	—	17·1	17·0
0–1 in. . . .	10·0	9·6	20·8	27·5	13·5	12·5	15·0
1–2 in. . . .	11·6	10·5	15·6	19·6	13·0	11·5	14·9
2–3 in. . . .	13·7	8·0	14·1	17·0	13·4	10·9	13·4
3–4 in. . . .	8·5	7·2	13·1	15·9	11·1	11·7	13·2

THE OXYGEN CONTENT.

The oxygen content of the pools is influenced by several factors of which the numbers and relative proportions of plants and animals are the most important. During the night both plants and animals are using up oxygen, while during the day the former are giving it off to the surrounding water. Other factors are also important, such as the length of day, intensity of illumination and temperature, but their effects are mainly produced through their influence on the organisms inhabiting the pools.

The presence or absence of green plants is thus of paramount importance in determining the amount of oxygen present in a pool. The vegetation of the marsh pools includes flowering plants such as *Potomageton pectinatus*, and *Zostera marina*, various algæ such as *Ulva lactuca* and *Enteromorpha intestinalis*, also diatoms, peridinians and other green flagellates. None of the pools appears to be entirely devoid of plant life, a few small diatoms and filamentous algæ being present in all of them.

The Diurnal Variation in Oxygen Content.

An examination of the changes in the oxygen content was made throughout the hours of daylight in three types of pool, one containing large quantities of Enteromorpha, one containing diatoms only, and

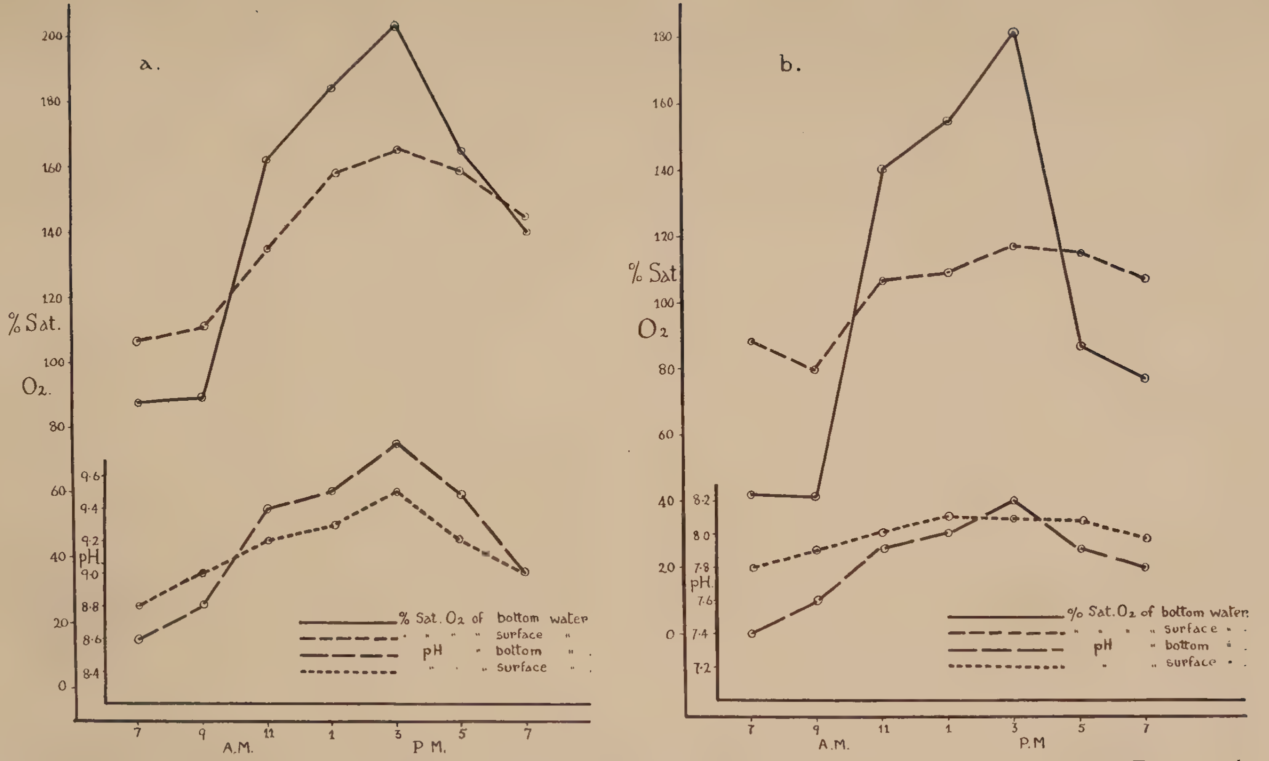


FIG. 11 *a* and *b*.— The percentage saturation with oxygen and the hydrogen ion concentration of the water of (*a*) Pool V containing Enteromorpha and Ulva ; (*b*) Pool IX containing diatoms.

one in which plant life of any kind was scarce. A bright day was chosen at the end of October when daylight began a little before 7 a.m. and finished just after 5 p.m. Observations were made every two hours from 7 a.m. to 7 p.m. The results are recorded in Figure 11, which gives the percentage saturation with oxygen in the three types of pool at the salinity and temperature recorded. Figure 11*a* gives the condition in Pool V, containing a mass of Enteromorpha. Both the top and bottom water show the same changes, a slow rise from 7 to 9 o'clock, when the sky was overcast, a rapid rise till 3 o'clock when the light intensity was at its maximum, followed by a fall in oxygen content. Unfortunately it was not possible to extend the observations during the night, but without doubt this fall would have continued throughout the hours of darkness, until a minimum value was reached before dawn the next morning. The bottom water shows a rise of 110% while the surface water shows a rise of only 59%. This discrepancy may have been due to the fact that a strong breeze was blowing, causing loss of oxygen from the surface, but is more likely to have been caused by the concentration of the algæ at the bottom of the

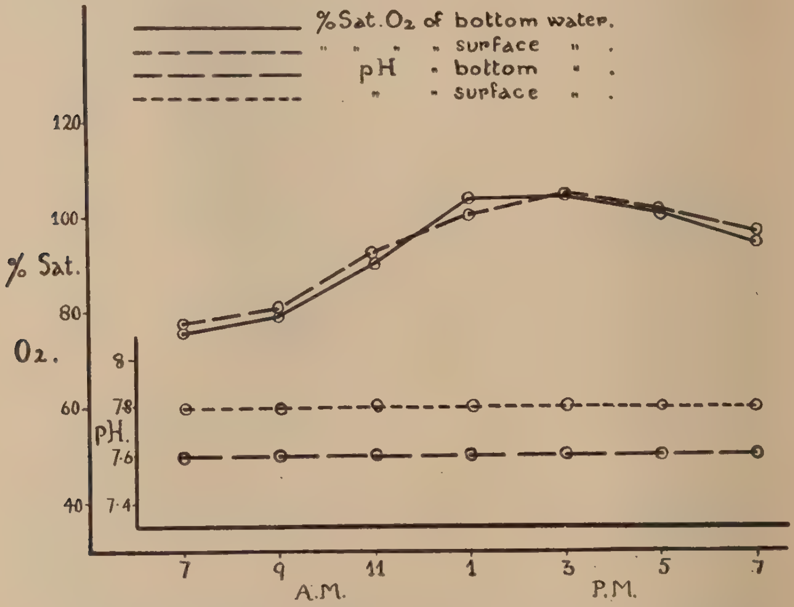


FIG. 11 *c*.—The percentage saturation with oxygen and the hydrogen ion concentration of the water of Pool XIII containing no plant life, during the hours of daylight on October 27th, 1933.

pool. This is further suggested by the fact that the oxygen content of the bottom water had fallen below that of the surface water during the night owing to the amount used up by the plants and animals at the bottom in respiration. Figure 11*b* gives the conditions in Pool IX, containing diatoms only. The curves follow the same general form as the last, but the great power of diatoms to saturate the water is well marked. In October diatoms are by no means at their maximum numbers, yet in this pool the increase in saturation of the bottom water was 142%, actually greater by 32% than that in Pool V crowded with Enteromorpha. This can be explained by the small size of the individual diatoms and the absence of storage space in their tissues, causing minute bubbles of oxygen to be liberated which pass at once into solution, as Butcher, Pentelow and Woodley (1931) have pointed out. In Pool XIII (Fig. 11*c*) where the plant life is scarce, consisting largely of minute green flagellates, the increase in oxygen is much less and the water hardly supersaturated even at 3 p.m. The curves for both top and bottom water are almost the same, rising from 77% to 104%, an increase of only 27%.

These observations are of interest when compared with those of Gessner (1931) for salt-marsh pools on Hiddensee. There many of the fresher pools are densely packed with *Ranunculus baudottii*, yet in May Gessner, making observations at midday and at midnight, found a change of only 50%, while even at midday the water was only slightly supersaturated. Pool V, containing Enteromorpha, shows a change of from 59 to 110%, with a shorter day and a lower light intensity, which suggests that algæ, as well as diatoms, possess the power of saturating the water with oxygen to a much greater degree than the higher plants.

Changes in Oxygen Content during longer periods.

The oxygen content of the pools at the same hour varies greatly from day to day, and this variation depends largely on the intensity of illumination and the temperature at the moment of sampling. The hours of sunshine have been taken as a measure of the intensity of illumination. These records are for the nearest meteorological station, North Berwick, eight miles away, and three sources of error arise : (i) the local conditions at Aberlady ; (ii) the distribution of sunshine during the day (two days having the same number of hours of sunshine might have it either in the morning or afternoon, and this difference would be shown in the oxygen samples made at midday, but not in the sunshine record) ; (iii) the hours of sunshine are not an accurate measure of the intensity of illumination. On the whole, however, it will be seen that the amount of oxygen present in the pools depends fairly closely on the number of hours of sunshine.

Figure 12 shows the oxygen content in percentage saturation of two pools during June, 1931. Curve A gives the conditions in Pool V rich in

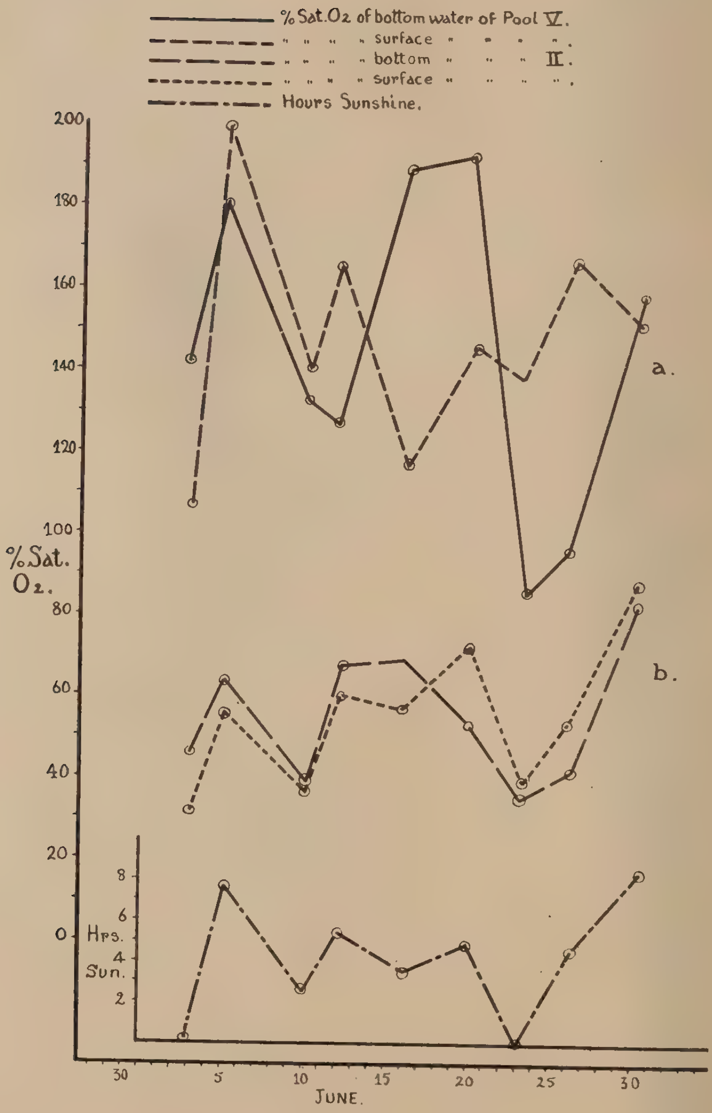


FIG. 12.—The percentage saturation with oxygen of the water of (*a*) Pool V containing much green weed, and (*b*) Pool II containing a few diatoms only.

algæ, and Curve B the conditions in Pool II with no large algæ and few diatoms, but with a fauna of Gobius, Gasterosteus, Corophium, Carcinus, Crangon, Neomysis and Nereis. In Pool V at midday the water is between 100 and 200% saturated with two exceptions, on June 23rd and 26th. On the first date the day was overcast and raining, and on the second, although four hours' sunshine is recorded, it is probable that they occurred in the afternoon after the water samples had been taken. In Pool II, on the other hand, the water is never fully saturated, and often has an oxygen content of 2·5 cc. per litre, less than 40% saturated, even at midday. The hours of sunshine are also recorded, and it can be seen that with the single exception already mentioned the oxygen curves follow fairly accurately that for the hours of sunshine.

The Alkali Reserve.

The alkali reserve of any natural water is important, as on it largely depends the amount of carbon dioxide available for photosynthesis, thus influencing indirectly the supply of oxygen in the pools. It is also closely related to the hydrogen ion concentration.

The alkali reserve of water from the open sea lies between ·0023 N. and ·0026 N., but that of fresh water varies between wide limits ; at Aberlady the alkali reserve of the Peffer Burn is ·0040 N. The water of the salt-marsh pools is derived from direct rainfall, from the sea, and from the land by drainage. It is clear therefore that alterations in the relative volumes of water contributed by these three sources will produce corresponding changes in the alkali reserve of the water of the pools. In addition the amount of evaporation will affect the alkali reserve to a lesser extent.

Direct Rainfall.

The effect of direct rainfall is, naturally, to reduce the alkali reserve of the surface water by dilution, at the same time as the salinity is reduced. If the rain is accompanied by wind the bottom water will also be affected. The effect of rain alone is clearly seen both in Figure 14 and in Figure 15, after the rain of April 24th, when both the alkali reserve and the salinity of the surface water fell considerably. The effect of prolonged wet weather is to lower the alkali reserve of all the water in the pools very considerably. In 1931 after a very wet spring 3·95 inches of rain fell in the first fortnight of June, and the alkali reserve of the pools became very low. The following table gives the values for some of the pools. As soon as the rain ceased the alkali reserve began to rise owing to the effects of drainage water which had previously been masked by the rainfall.

TABLE VIII.

		Date.			
Pool		June 5th.	16th.	20th.	26th.
II	Surface water	·0012 N.	·0025 N.	·0028 N.	·0031 N.
	Bottom water	·0012 N.	·0034 N.	·0034 N.	·0034 N.
X	Surface water	·0025 N.	·0049 N.	·0057 N.	·0059 N.
	Bottom water	·0023 N.	·0052 N.	·0064 N.	·0072 N.
IX	Surface water	·0009 N.	·0017 N.	·0019 N.	·0027 N.
	Bottom water	·0009 N.	·0017 N.	·0018 N.	·0031 N.

Sea Water.

The effect of a tide entering a pool is usually to lower the alkali reserve. This is clearly shown in Figure 13 for Pool XI during April and May, 1933. In the periods between the high tides the alkali reserve rose steadily under the influence of drainage water, but there is a sharp drop each fortnight coinciding with the first of each group of tides. The amount of lowering depends on the alkali reserve of the water entering the pool, and that in turn depends on the ratio between the amount of sea and

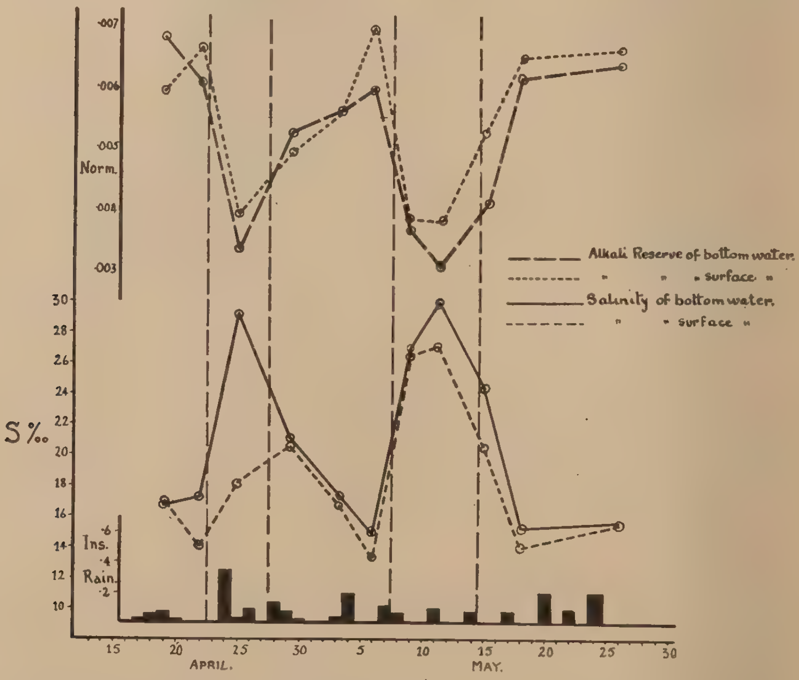


FIG. 13.—The effect of evaporation on the alkali reserve of the water of Pool XI during the spring of 1933. The vertical lines mark the limits of the periods during which tides entered the pool.

river water. As already stated, the alkali reserve of sea water lies between ·0023 N. and ·0026 N., while that of the water of the Peffer Burn is about ·0040 N. For instance, on April 25th the alkali reserve of the bottom water of Pool XI fell to ·0033 N., while on May 11th it fell to ·0030 N. In the first instance, following heavy rain in the night, there was a greater proportion of river water than in the second, so that the alkali reserve did not fall so much. Again the estuarine water during a period of high tides may not have a uniform alkali reserve throughout. Both on April 25th and May 11th the alkali reserve of Pool XI was higher at the surface than at the bottom, showing that the river water had flowed out on the surface of the sea water. This is confirmed by the lower salinity of the surface water.

Drainage water.

The effect of drainage water on the alkali reserve of the marsh pools can sometimes be clearly followed. The water reaching the marsh from the land percolates through sandy soil rich in the remains of marine shells on the right bank, and on the left through soil overlying and partly derived from limestone strata, consequently it has a high alkali reserve. During the spring of 1933 the effect of drainage water was clearly marked. The early part of April was wet, but later little rain fell though drainage water

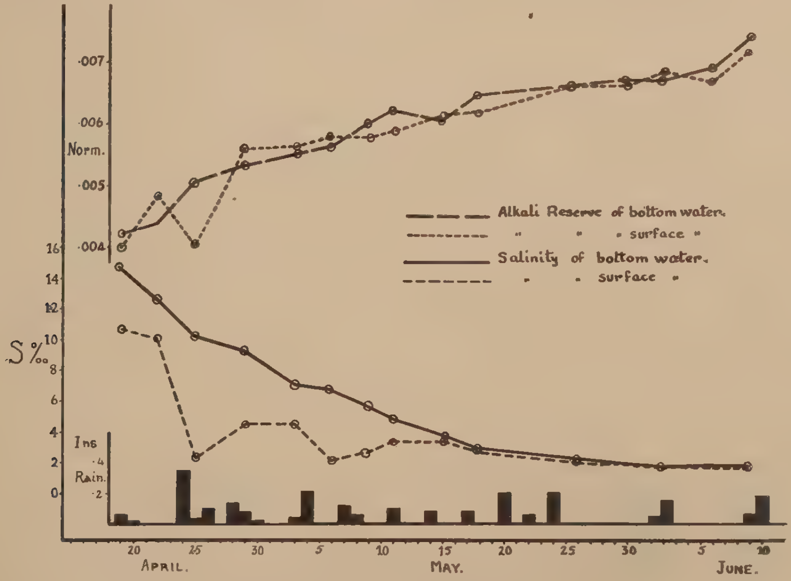


FIG. 14.—The effect of drainage water on the alkali reserve of the water of Pool XIII during the spring of 1933.

continued to be abundant, and, percolating through the soil, lowered the salinity of the pools at the same time as it raised the alkali reserve. A good example of this is shown in Figure 14 for Pool XIII. A tide entered the pool on April 14th, and five days later the salinity of the surface water was 10·6°/$_{oo}$, and the bottom water 14·8°/$_{oo}$. After that, until June 17th, when the records stopped, the salinity fell steadily and the alkali reserve rose from an average of ·0041 N. to ·0073 N. Similar results were obtained for Pool I on the left bank, and are illustrated in Figure 15. Here, as the salinity fell (although the pool was gradually drying up), the alkali reserve rose from ·0052 N. to ·0098 N.

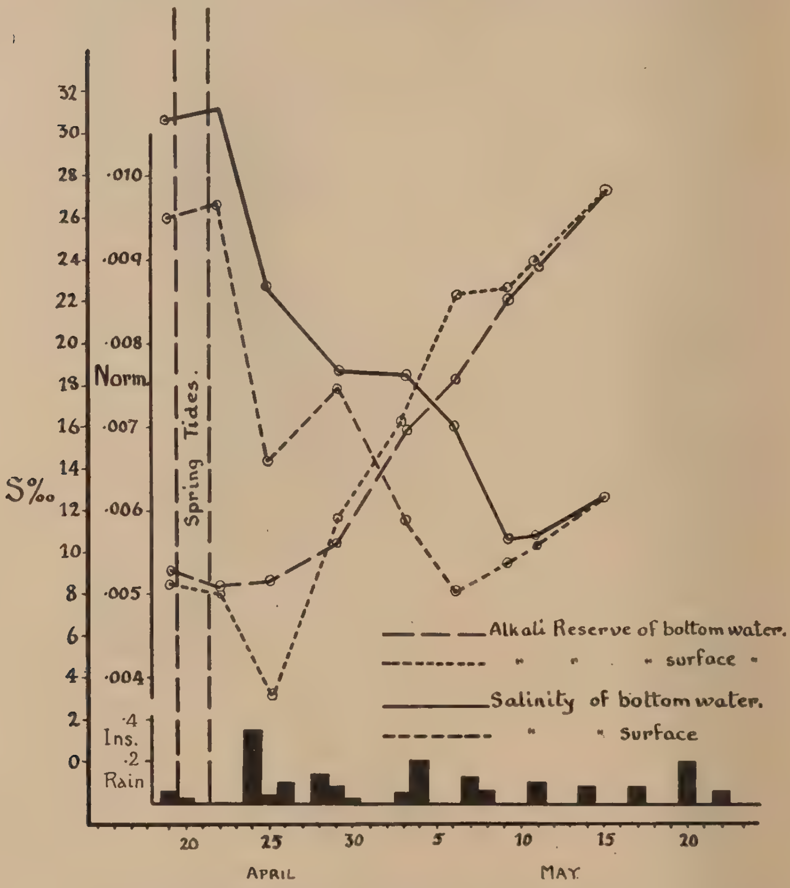


Fig. 15.—The effect of direct rainfall, drainage water and evaporation on the alkali reserve of the water of Pool I during the spring of 1933.

Evaporation.

The effect of evaporation is to raise the alkali reserve as well as the salinity, and this effect is shown in Figure 16 for Pool III during May and June, 1933. A high tide entered the pool on May 11th, raising the salinity to 30·6 and 32·2°/$_{oo}$, and lowering the alkali reserve to ·0032 N. and ·0028 N. for the surface and bottom water respectively. After that the salinity and the alkali reserve rose steadily until June 17th, when the records stopped. The final salinities were 38·0 and 37·6°/$_{oo}$, and the final alkali reserve for both top and bottom water was ·0034 N.

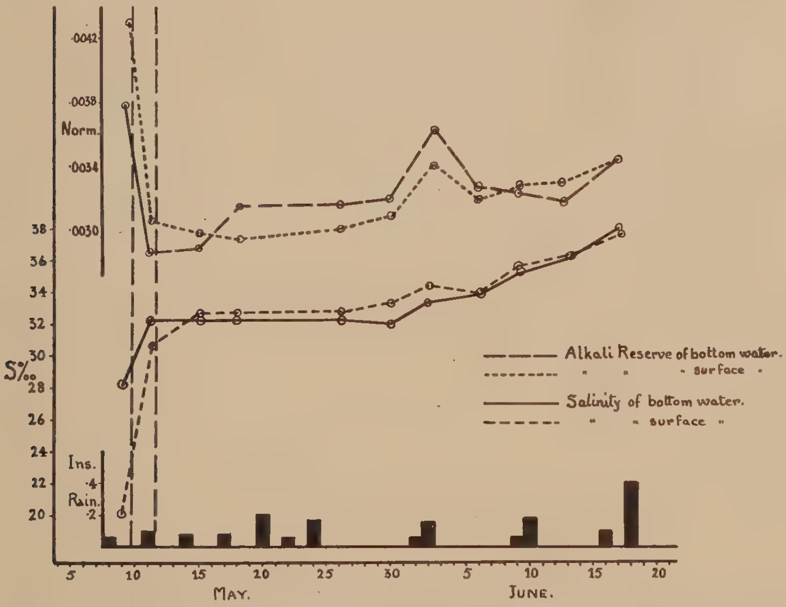


Fig. 16.—The effect on the alkali reserve of the water of Pool III of a tide entering it during the spring of 1933. The vertical lines mark the limits of the periods during which tides entered the pool.

The Hydrogen Ion Concentration.

The hydrogen ion concentration in a particular pool depends on the alkali reserve of that pool, and on the carbon dioxide tension in the water. The carbon dioxide tension, on the other hand, depends on the intensity of photosynthesis and on the amount of animal life in the pool. Since the alkali reserve is usually high and the pools are not, as a rule, crowded with animal life, the chief factor responsible for the control of the hydrogen ion concentration is the amount of vegetation present.

Diurnal variation.

The hydrogen ion concentration, being closely connected with the amount of photosynthesis, may be expected to show a diurnal variation with a minimum value (i.e. maximum pH) at the same time as the maximum oxygen content of the pools, and a maximum (minimum pH) during the night, when the respiration of both plants and animals tends to saturate the water with carbon dioxide. Such diurnal variations are shown in Figure 11 along with the percentage saturation with oxygen. In Figure 11*a* the condition is shown in a pool containing much Enteromorpha, and in Figure 11*b* the condition in a pool containing diatoms only. In both the pH curve follows the oxygen curve, rising to a maximum at 3 p.m. and falling again towards evening. The maximum rise in both pools is about pH 1·0, and is greatest in the bottom water, which also shows the greatest rise in oxygen content. In Figure 11*c* the conditions in a pool containing very little plant life are shown. The increase in oxygen is very much less than in the other pools, and the hydrogen ion concentration is unchanged. In this pool the alkali reserve was much higher, ·0072 N. as against ·0031 N. in the others, and was probably instrumental in reducing the effect of such photosynthesis as took place in this particular pool.

The Hydrogen Ion Concentration during Longer Periods.

A similar relationship between the hydrogen ion concentration of a pool and the oxygen content can be shown for longer periods of time.

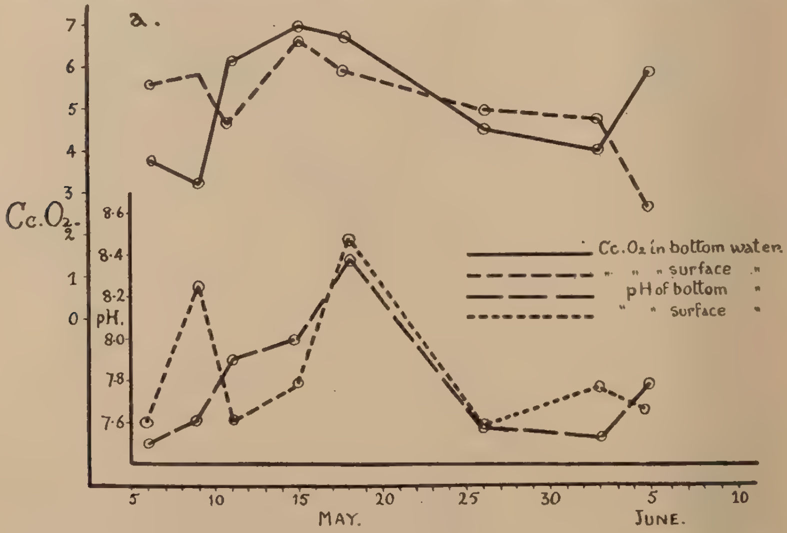
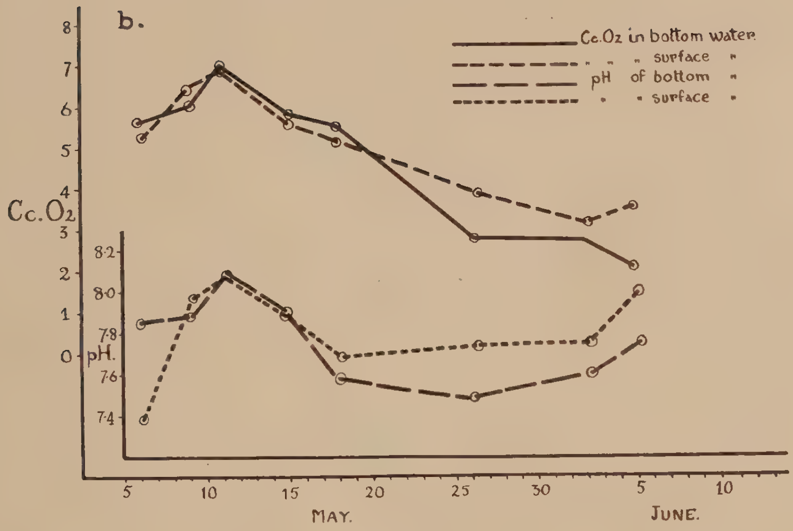
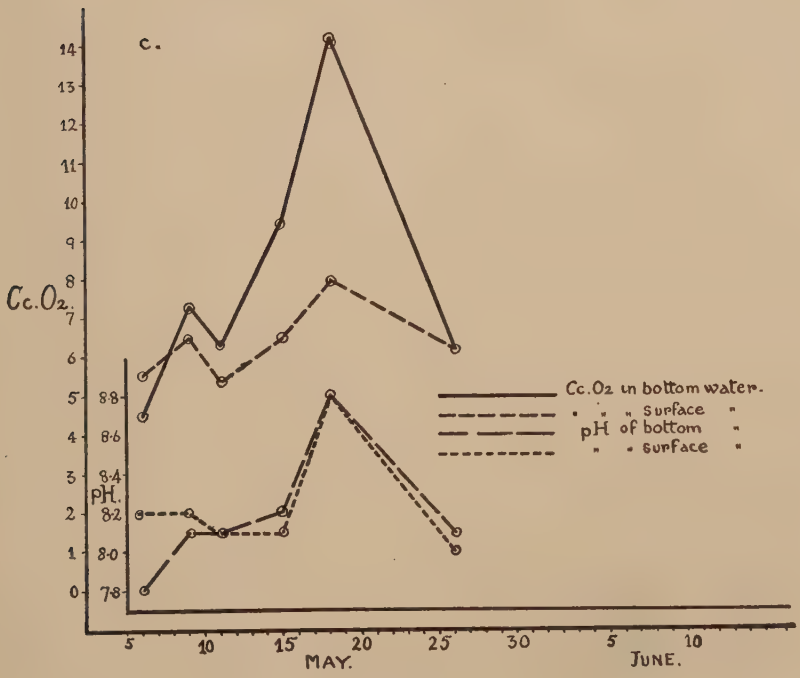


FIG. 17.—The changes in hydrogen ion concentration and in the oxygen content of the water of three pools during the spring of 1933. (*a*) Pool XIII.



(b) Pool V.



(c) Pool IX.

FIG. 17. (*contd.*)

In Figure 17 the conditions in three different pools all containing a considerable amount of plant life are given for the month of May and part of June, 1933. In all of them the oxygen and pH curves agree closely, the maximum and minimum values falling approximately on the same days.

The Range of Hydrogen Ion Concentration.

The total pH range in the marsh pools varies from a minimum of pH 6·8 to a maximum of 9·6, but these extreme values were not recorded from the same pool. The highest pH values are obtained in the pools with the greatest amount of weed. The following tables give values for the three pools previously discussed.

TABLE IX.

	Pool V. Enteromorpha.		Pool IX. Diatoms.		Pool XIII.	
Date.	Top pH.	Bot. pH.	Top pH.	Bot. pH.	Top pH.	Bot. pH.
5.6.31 . .	9·6	9·0	7·7	7·5	7·4	7·0
10.6.31 . .	8·0	8·8	7·6	7·4	7·2	7·2
23.6.31 . .	9·2	9·2	8·2	7·7	7·4	7·4
19.4.33 . .	8·0	8·0	7·9	8·0	7·5	7·4
9.6.33 . .	8·2	8·2	8·2	8·0	7·6	7·6

THE TEMPERATURE.

The Daily Variation.

The daily variation of temperature in the pools was not studied exhaustively since no night observations were made. The following figures are typical for the hours of daylight.

TABLE X.

Date.	Pool.	Depth.	Temperature in °C. Max.	Min.
June 14th, 1932 . . .	V	Top	21·5	14·0
		Bottom	19·0	13·5
October 27th, 1933 . .	V	Top	5·5	4·5
		Bottom	6·0	5·0

The Seasonal Variation.

During cold weather all the pools of the marsh may be covered with a sheet of ice, the thickness of which depends on the salinity of the surface layer of water. This is particularly marked when the frost follows a period of calm wet weather and a layer of almost fresh water lies on top of the salter water in the pools. During hard frost the pools may be covered with one to four inches of ice for several weeks at a time, as in January, 1933.

During the summer the average temperature is considerably above that of the open sea, and the following temperatures are typical for the months of June and July.

TABLE XI.

Depth.	Temperature °C.				
Surface water .	24	27	24	25	27
Bottom water .	23·5	26	25	24	24
Surface mud . .	23	24·5	25	24	24

Higher temperatures have often been recorded in shallow pools densely crowded with weed. The highest figure was 32·5° C., on June 17th, 1933. This temperature did not appear to be harmful to the animals living among the weed, *Sphæroma rugicauda*, *Melita palmata*, *Hydrobia ulvæ* and *Limopontia capitata*, all of which appeared normally active.

Temperature in the Mud.

The temperature in the mud varies very little from that of the overlying water, but may show a lag of a degree or two with rapidly rising or falling temperatures.

When, however, the pools are dry, then the temperature of the mud is often very high at the surface and progressively lower at greater depths. The following table gives some temperatures at different depths in the mud of dry pools on June 17th, 1933, when the sun temperature was 30·5° C. and the shade temperature 25° C.

TABLE XII.

Depth Below Surface.

½ inch.	2 inches.	4 inches.
31·5	22·0	—
28·0	22·0	—
29·0	24·0	18·0
28·0	22·5	18·0
31·0	26·0	22·0
29·0	26·0	24·0
33·0	27·0	24·0

DISCUSSION.

The particular interest of a salt-marsh lies in the fact that it is one of the meeting-places of the fresh-water and marine faunas. As a result of prolonged acclimatisation a specialised brackish-water fauna has been derived from both sources, much of which seems to have become incapable of living for any length of time in its old environment. A similar specialised fauna is found in estuaries, land-locked seas, lagoons and salt-marshes all over the world, and, to a lesser extent, in inland saline lakes. In temperate regions the number of species forming the community is relatively small, but in tropical waters it is very large, the fauna of any big estuary or brackish lagoon showing numerous endemic species as well as many others of wider distribution (Annandale, 1922).

Remane (1934) gives graphs to show that the number of marine species in brackish water of varying salinity decreases steadily as the salinity falls. Similarly the number of fresh-water species falls as the salinity rises. Where the distribution curves overlap the minimum number of species occurs. Contrary to what one might expect, this poor fauna is not found where the water is of intermediate salinity at about 17·5$^\circ/_{\circ\circ}$, but lies at a point between 5 and 8$^\circ/_{\circ\circ}$. Although in a large estuary or body of water such as the Baltic this observation can be easily checked, in a salt-marsh the salinity changes are so large and erratic that it is difficult to classify the pools on a salinity basis. It is, however, clear that the pools with a salinity of between 15 to 20$^\circ/_{\circ\circ}$ support the richest fauna from the point of view of number of species. In pools entered by fewer tides fewer species occur, *Nereis diversicolor*, *Corophium volutator* and *Gammarus duebeni* forming the greater part of the fauna, while in the freshest pools again, although the marine animals have disappeared, the number of species is again larger owing to the predominance of fresh-water animals.

In discussing a problem such as this the need is at once felt for some convenient basis of classification of the environment. An attempt has been made to supply this by Redeke (1922 and 1931), who takes the chlorine content of the water as the limiting factor in the distribution of members of the brackish-water fauna. The following is his scheme of classification :

		Cl. gm. per lit.	S$^\circ/_{\circ\circ}$.
Fresh Water		0·0— 0·1	0·0— 0·2
Brackish Water	Oligohaline	0·1— 1·0	0·2— 1·9
	Mesohaline	1·0—10·0	1·9—18·6
	Polyhaline	10·0—17·0	18·6—31·8
Sea Water		17·0+	31·8+

These divisions, he states, correspond closely to the differences in the fauna, no matter what type of brackish water is investigated.

The oligohaline region has few characteristic animals, the bulk of the fauna being formed by fresh-water species which are able to withstand a certain amount of salt. Redeke (1922) cites *Eurytemora affinis* and *E. velox*, *Cordylophora lacustris* and *Dreissenia polymorpha* as typical of this region. To these should be added *Gammarus duebeni*.

The mesohaline zone is inhabited by the most characteristic brackish-water species, such as *Brachionus mulleri*, *Manyunkia estuarina*, *Nereis diversicolor*, *Sphæroma rugicauda*, *Corophium volutator*, *Neomysis vulgaris* and *Gobius microps*, which, although found also in other regions, reach their maximum numbers in the mesohaline zone.

Just as the bulk of the oligohaline fauna is composed of fresh-water species, so the greater part of the polyhaline fauna is derived from the sea. *Corophium crassicorne*, *Gammarus locusta* and *Eurytemora hirundo* are given by Redeke as typical polyhaline animals.

Although this classification has been found to be satisfactory when applied to lagoons and large estuaries, when an attempt is made to apply it to small bodies of water such as salt-marsh pools it breaks down completely owing to the fact that every tide and every shower of rain alters the composition of the water in the pools, which may pass from a polyhaline to an almost oligohaline condition in a few days, so that only animals which are able to withstand the whole range of salinities for an appreciable length of time will be able to survive permanently in the small pools of a salt-marsh. Under these circumstances isolated observations on the salinity of such pools are useless as indicators of the conditions under which an animal is living. Redeke himself admits the breakdown of his scheme when dealing with the conditions in small estuaries where the salinity during the intertidal period ranges from almost pure sea water to fresh water. As a consequence of this the salinity of the pools at Aberlady can only be regarded as controlling between wide limits the distribution of the fauna. The average conditions of salinity throughout the year show that the greater part of the Aberlady marsh belongs to the mesohaline zone, and as such supports a typical brackish-water fauna. All the characteristic species given by Redeke are present, and, in addition, a number of species which cannot be regarded as typical since they do not occur in estuaries. This difference is correlated with one important characteristic of salt-marsh pools, namely, the stillness of the water. This absence of movement makes it possible for fresh-water animals in particular, living in neighbouring ponds and lakes, to invade the less saline pools of the marsh. At Aberlady the pools of low average salinity are limited in size and number, and are liable to be invaded by sea water, so that the fresh-water fauna found in them is sparse. The majority of the species can be traced to the neighbouring ponds from which successive waves of colonisation take place during each period of low salinity. Certain brackish-water species also only occur in still water. Some of these such as *Aëdes detritus* are directly dependent on lack of current, others such as *Chironomus aprilinus*, *Protohydra leuckarti* and *Cricotopus vitripennis* appear to depend on a substratum of soft mud, which is most commonly laid down in still water, while yet others are found only on certain kinds of algæ. Some of these algæ are non-rooting; and can occur only in still water. *Melita palmata*, *Procladius choreus*, *Alderia modesta* and *Limopontia capitata* are species which, absent from estuaries, are dependent on marsh vegetation.

One point of widespread interest is suggested by an examination of any fauna list of brackish-water species, and a consideration of the relative proportions between the fauna derived from the sea and from fresh water. Once the power to colonise a new type of habitat has been developed, and the old habitat entirely abandoned, it is more difficult to return to the original environment than it was in the beginning to become acclimatised to the new. Colonisation of fresh water began in the Devonian (Sollas, 1905), has proceeded ever since under suitable circumstances, and is proceeding at the present day. From this steady influx of marine species first into brackish, then into fresh water, has been derived the present-day fauna of rivers and lakes. Yet during all that time few species have returned to brackish water, fewer still to the sea. By far the larger number of animals in brackish water are derived direct from the marine fauna, and only a few from the fresh water. Of these few the majority belong to the insects which, being encased in a chitinous covering, are relatively independent of the environment.

When the changing conditions in the marsh are compared with those of the open sea it is possible to understand some of the difficulties which confront animals attempting to colonise such an environment. The ocean shows small seasonal and daily variations in salinity, in oxygen content, in hydrogen ion concentration, and in temperature ; the salt-marsh water is constantly changing, showing in twenty-four hours far larger fluctuations than can be found in the open sea in six months. The gap between the two extremes is partially bridged by the conditions found in inshore waters and the mouths of estuaries, but there the lines of retreat from too unfavourable conditions are always open. In small estuaries, for instance, the change from salt to almost fresh water is rapid, occurring twice in the twenty-four hours, but animals attempting to gain a footing there have three ways of escape from the extremes : they may retreat down the estuary with the falling tide and return again with the flood as do crustacea such as *Praunus flexuosus*, or they may burrow deep in the mud as do worms and molluscs such as *Arenicola marina* and *Scrobicularia* *piperata*, and so escape both the high salinity of full tide and the low salinity of the river water; or again they may allow themselves, like *Carcinus maenas*, to be left behind by the falling tide to take refuge in crevices or under moist weed, and so avoid the lowest salinities. The animals in the salt-marsh pools are offered no alternatives. They cannot go out to sea, they cannot permanently remain deep in the mud, they cannot leave the pools for an indefinite period; if they are to survive at all it must be by their power of adaptation to circumstances and not by avoiding them.

The greatest difficulty for the salt-marsh animals is that of the changing salinity owing to the osmotic effect on their body fluids. A few animals such as *Gasterosteus aculeatus* and *Anguilla vulgaris* are known to be able to withstand sudden changes from salt to fresh water. It is animals such as these that are the most successful colonisers. In many instances, however, it has been shown that marine animals can be acclimatised to low salinities and even to completely fresh water by lowering the salinity gradually (Beudant, 1816). The success of the experiment depends, however, on the slow rate of change, a sudden lowering of the salinity by even a few parts per thousand causing death. It is just this problem of the rate and degree of change which is so vital in the salt-marsh, since the fluctuations there are so great from day to day.

Early work on the body fluids of marine animals suggested that their osmotic pressure was always identical with that of sea water, but recent work has established that in nearly every case the osmotic pressure is very slightly higher than that of the surrounding medium. When, however, the salt content of the environment is reduced by dilution this high osmotic pressure is not maintained, it drops rapidly owing both to the passage inwards of water and to loss of salts, and, if the dilution is great enough and the time of exposure long, death follows. In those animals able to withstand large changes of salinity, however, this is not the case. The osmotic pressure is maintained at a level well above that of the surrounding water, very little swelling takes place and the animals remain active indefinitely in the diluted medium. A comparison between closely related forms from the open coast and from estuaries, such as *Nereis cultrifera* and *Nereis diversicolor* (Beadle, 1931), shows that the fall in osmotic pressure and the swelling due to uptake of water occurs in the animals from both localities, but that in the brackish-water species the process is quickly arrested and no loss of activity ensues. Further investigation shows that this arrest is accompanied by a rise in the oxygen consumption, which reaches a maximum and then gradually falls to a level somewhat above the normal and continues there indefinitely. This increase in oxygen requirements suggests that the difference between the external and internal osmotic pressure can only be maintained by the expenditure of energy on the part of the animal. An interesting point arises here, namely, that an initial rise in oxygen consumption was also present in *Nereis cultrifera*, but was not maintained as the osmotic pressure began to fall, suggesting that marine animals are potentially able to control the osmotic pressure of the internal medium. Schwabe (1932) has recently shown that the ability to maintain osmotic control in brackish water is not equally strong at all periods of the life history, but depends on the physiological condition of the animal at the time. His experiments show that during periods of prolonged hunger the osmotic pressure of the body fluids of various crabs kept in diluted sea-water falls slowly until the animals become distended with water and die. He also shows that after moulting the osmotic pressure drops considerably below the normal in diluted sea-water and that the same thing occurs during the period when the female is carrying eggs. This last observation probably explains why, although several kinds of crustacea penetrate right into fresh water, they are never known to breed there (Gurney, 1923 ; Annandale, 1922 ; Peters and Panning, 1933).

The rise in the oxygen requirements shown by Schleiper (1931), and also by Beadle (1931), constitutes a second difficulty for salt-marsh animals. Beadle shows that *Nereis diversicolor*, on being moved from 100% to 16·5% sea water, more than doubles its oxygen requirements, while Schleiper gives similar figures for *Carcinus maenas*, and it is probable that a comparable rise occurs in all brackish-water animals. Schwabe (1932) has also shown that keeping *Carcinus maenas* under conditions of low salinity combined with low oxygen tensions has a deleterious effect on the activity of the crab, and that the osmotic pressure of the blood of such animals falls considerably lower than that of animals subjected to low salinities with a plentiful supply of oxygen. In the salt-marsh temperatures are often high, increasing the activity of the animals and reducing the oxygen capacity of the water. Oxygen, although often abundant during the day, is scarce during the night, and it is conceivable that after rain this oxygen lack might have a disastrous effect on the animals, already faced with the difficulties of diluted salinities.

An observation by Bateman (1933) may have some bearing on the problem of survival in brackish water. He states that in captivity *Carcinus maenas* placed in half-strength sea water can only survive between pH 6·0 and 9·0. Above pH 9·0 death occurs within thirty-six hours. In the marsh small crabs appear to be evenly distributed, and are found among the weed in pools with a pH as high as 9·6. It is, however, only during the day that this high value is found, during the night it may be as low as pH 8·0. Either Carcinus can survive a high pH over short recurring periods, or, under natural conditions, changing hydrogen ion concentrations have no effect. It may be significant that in the Aberlady salt-marsh the pools with the highest pH are also the pools with the highest salinity. It is generally considered that normal variations in the hydrogen ion concentration of the open sea do not affect the fauna adversely (Harvey, 1928), but in an atypical marine habitat such as a salt-marsh, showing large fluctuations, the hydrogen ion concentration may be of considerable importance.

Von Martens (1857) has suggested that a possible reason for the greater number of animals of marine origin in brackish and fresh water in the tropics lies in the more even temperature conditions throughout the year. The work of Giard (1883) showing that Gasterosteus is only able to withstand sudden changes from fresh to salt water and vice versa provided that the temperature is kept even, supports this view. Whether the temperature is the principal factor involved in successful colonisation of brackish water is another matter. The temperature variations in the temperate zone are certainly much greater than in the tropics, not only in fresh water but also on the seashore. Southern (1915) gives 16·5° C. as the maximum seasonal variation, and 4·1° C. as the maximum variation in twenty-four hours, for the water of Ballynakill harbour. The changes in rock pools must be much greater. Many of the colonisers of salt-marshes live normally in this littoral zone, and are already acclimatised to very variable temperatures. An increase in temperature leads to an increase in the rate of respiration and to a lower saturation point of the water with oxygen. On the other hand, the rate of photosynthesis is increased and the water of the pools is readily supersaturated, so that only in those devoid of all vegetation would an oxygen shortage be likely to occur during the summer. The density of population is sometimes great, but the size of the animals is small, so that it is doubtful whether high temperatures alone present any difficulties to salt-marsh animals derived from the littoral zone.

Little is known of the effect of other factors on the vitality of animals in brackish water. Pantin (1931) finds that the presence of calcium in the water has a marked effect on the power of *Gunda ulvæ* to withstand low salinities and suggests that the distribution of Gunda is limited to small streams of hard water; 15% of the calcium found in sea water appears to be sufficient for the needs of the animal. Although the amount of calcium in the water at Aberlady was not directly investigated, in view of the situation of the marsh on an old raised beach in close proximity to calciferous strata, it is permissible to assume that the alkali reserve of the water consists almost entirely of calcium salts. If this is so the calcium content of the water has not been observed to fall seriously below 50% of that found in pure sea water, and in many instances, when drainage water is abundant, is three or four times as great. Under the circumstances it is unlikely that calcium shortage plays any part in the economy of a marsh such as that at Aberlady. In other marshes, however, situated in peat districts, as on the west coast of Scotland and in Ireland, it may be of considerable importance, especially as it has been shown by Ellis (1933) that in *Nereis diversicolor*, a typical salt-marsh species, the absence of calcium in the water causes an increase in weight, followed by loss of movement greater than that occurring ordinarily in diluted sea water, and that addition of calcium instantly starts a return to normal conditions.

SUMMARY.

The salt-marsh under investigation is situated at Aberlady Bay on the south shore of the Firth of Forth, fifteen miles east of Edinburgh.

The marsh is small and occurs at the mouth of a stream. The character of the soil on the two banks differs, being on the one side muddy with permanent pools, and on the other sandy, so that the pools tend to drain dry. The vegetation of the pools is variable, some containing species of Zostera, Ulva, Enteromorpha and Vaucheria, others having only diatoms.

The surface of the marsh has a characteristic fauna of species such as *Orchestia gammarella*, *Paragnathia maxillaris*, *Podura marina*, and *Dichirotrichus pubescens*. The pools can be divided into two groups, those having a low average salinity of less than $5\ ^{\circ}/_{\circ\circ}$, and those having an average salinity of 15 to $20^{\circ}/_{\circ\circ}$. In the former brackish-water species such as *Aëdes detritus*, *Gammarus duebeni* and *Helophorus viridicollis* occur in numbers as well as fresh-water species such as *Agabus bipustulatus*. In addition, during periods of very low salinity, species such as *Culex pipiens* and *Limnæa truncatula* colonise the pools from the neighbouring marshes. In the pools of higher salinity *Gobius microps*, *Neomysis vulgaris*, *Corophium volutator* and *Nereis diversicolor* are common. *Alderia modesta*, *Limopontia capitata* and *Protohydra leuckarti* also occur in certain pools in large numbers. Marine forms such as *Macoma balthica*, *Mya arenaria* and *Arenicola marina* are also found.

Detailed observations were made on the conditions under which the animals in the pools are living.

The salinity of any pool is determined by the salinity of the water entering it at the last high tides and by the subsequent weather conditions. In hot weather during the summer the salinity of some pools may be as high as $40^{\circ}/_{\circ\circ}$, in wet weather as low as $8^{\circ}/_{\circ\circ}$. Other pools reached by fewer tides fluctuate between 15 and $0{\cdot}5^{\circ}/_{\circ\circ}$.

The oxygen content of the water depends largely on the amount of vegetation in the pool. Large daily fluctuations take place, the water on a sunny afternoon being as much as 200% saturated, and in the same pool at dawn as little as 40%.

The alkali reserve of the pools is high, being largely derived from drainage water percolating through an old raised beach behind the marsh. It may reach as high a value as ·0098 N., but a tide reaching the pool may lower it to ·003 N. During very wet weather it may be as low as ·0009 N.

The hydrogen ion concentration varies between pH 6·8 and 9·6, depending on the amount of vegetation and on the hours of sunshine.

During the summer the temperature may reach 32° C., while in winter even pools of high salinity may be frozen over for several weeks at a time.

The composition of the fauna and the relationship of the conditions to the life of the animals is discussed in connection with recent work on the physiology of some of the inhabitants of brackish water.

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The Biology of *Balanus balanoides.* III. The Soft Parts.

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With 4 Figures in the Text.

CONTENTS.

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In the first paper of this series an account was given of the growth of this species, and its variation with age, season and tidal level. The size of the barnacles was expressed in terms of the external volume of the shell, as determined from measurements of its length, breadth and height, usingthe formula $\text{Vol.}=0{\cdot}065\ \text{Ht.}\times(\text{Length}+\text{Breadth})^2$, (Moore, 1934, p. 852). So far as the shell was concerned, there was a period of rapid growth during the summer, followed by a period of little or no growth during the winter months. The first part of the present paper comprises an account of the corresponding changes in the soft parts of the barnacles.

Runnström (1925) states that the spat which settle in the early summer, grow very rapidly during their first summer, and do not develop more than rudimentary gonads until their second autumn. Because of the existence of this vegetative year, and because thereafter the gonads (and later, the larvæ in the mantle cavity) form a considerable proportion of the bulk of the tissues a distinction had been made throughout the work between immature first-year animals and those of two or more years old which are sexually mature. Actually it was found that in some special cases the vegetative first year was omitted. The distinction between first-year and older barnacles was made by means of differences in their colour as has been described in another paper (Parke and Moore, 1935). Most of the material was collected in Port Erin Bay in the locality previously used (Moore, 1934, p. 852). It was taken from three levels, B.1 just below mean sea level and representing the lower-zone type of barnacles for this locality;

B.2 between this and mean high water of neap tides, and representing the principal barnacle zone of the shore ; and B.3 slightly above mean high water of neap tides and representing the type of barnacles found at their extreme upper limit. Additional patches B.4 and B.5 at the same levels as B.1 and B.2 respectively comprised barnacles of a known age only, all others having been removed from the rock. Finally two sets of samples were taken at successive levels outside Bradda Head in a very exposed situation.

THE TISSUE WEIGHT AND ITS VARIATIONS WITH AGE, SEASON AND TIDAL LEVEL.

Barnacles were removed from the rocks, to which they were attached, with the aid of a knife, care being taken to remove the whole of the animal, and at the same time not to take any adhering fragments of rock. The material was then taken back to the laboratory where it was sorted according to its size, each size-group containing an adequate amount of barnacles for weighing. The number in each group varied from five to fifty according to their size. Either the whole or a part of each group was measured (length, breadth and height), and the whole group was then transferred to boiling water for a minute in order to coagulate the proteins and reduce loss of material in subsequent treatment. The barnacles were then decalcified in cold hydrochloric acid (one part in five), washed and transferred to a tared filter paper, then dried in a boiling-water oven and weighed. The resulting mean weight and volume for each group, as obtained in the successive seasonal samples, are given in Table I to V.

In Figure 1 is shown the normal growth of the shell at the three levels in Port Erin Bay (Moore, 1934, p. 858), and the corresponding growth of the tissues as obtained from these tables. The resulting curves are very complicated, and the possible explanations given are no more than tentative. The curve for the lowest level patch, B.1 is the simplest. The body weight rises fairly steadily up to the first spring. About July the weight begins to drop, reaching a minimum in August, after which it rises steadily again until the following spring, if the animal lives so long. In the case of these low-water barnacles, spawning takes place in the first season, the ova being liberated into the mantle cavity about mid-November, and the larvæ liberated into the sea in March. The average number of nauplii produced by a B.1 barnacle in its first year is 360 (see p. 270), and their weight, 0·27 mgm., is negligible in relation to the total weight of the barnacle. The drop of 50% in weight is connected with spawn production, but it also corresponds with the period of maximum sea temperature which occurs in mid-August.

At the middle and upper level, B.2 and B.3, no spawning takes place

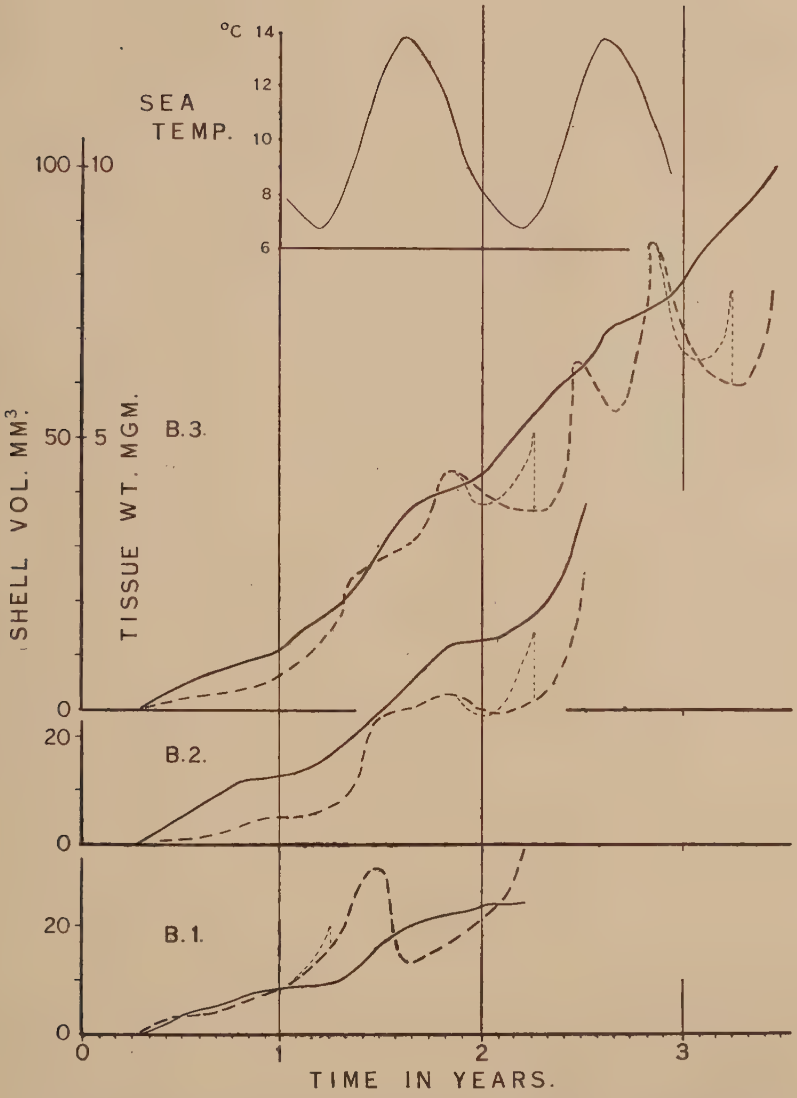

FIG. 1.—Growth of typical *B. balanoides* at Port Erin at low- (B.1.), intermediate- (B.2) and high-level (B.3), in terms of external shell volume (whole line) and dry weight of decalcified tissues (broken line). The lighter broken line indicates the weight values over the period when there were larvæ in the mantle cavity, as inferred from the known spawn output, but not shown in the main curve owing to wide spacing of readings at that period. The mean sea surface temperatures for Port Erin Bay are shown above.

in the first year. During this vegetative period body growth follows a very similar course to that on B.1, except that there is no actual summer drop in body weight, this being indicated merely by a temporary decrease in the rate of growth, and a corresponding flattening in the curve. In the case of B.3 in its third season, however, the summer drop in body weight is extremely pronounced, though less so than that in the first year on B. 1, and as the drop is in both cases subsequent to their first spawning, there would seem to be some connexion between this summer loss of weight and the condition of maturity of the barnacle.

In the case of B.1 there was only a small production of spawn and no loss of weight during the winter period of November–March when the larvæ were being carried in the mantle cavity. In both B.2 and B.3, on the other hand, where the larval production amounts to a considerable proportion of the total weight of the animal, there was a drop in weight immediately following the liberation of the ova into the mantle cavity. This drop is not due to the loss of the larvæ from the weighing, since they continued to be weighed along with the rest of the soft parts of the barnacles until the time when they were liberated into the sea. And since such a drop is not present in the first vegetative year in either group, it would appear that the maturation of the larvæ in the mantle cavity involves some expenditure of energy and corresponding loss of weight on the part of the barnacle. It should, however, be noted that the time at which this drop in weight occurs coincides with the period of minimum sea temperature. As soon as the larvæ have been liberated, the body weight rises steadily to its June maximum.

The cycle of changes in the weight of the body thus seems to resolve itself into two parts. The first is a simple condition of rapid increase during the spring and autumn, with a slower rate of growth during the summer and winter temperature extremes. Superimposed on this there is a slight drop in weight in winter in those animals which are maturing larvæ, and also in these mature animals a considerable loss of weight during the following summer period of high temperature.

With regard to the effect of tidal level, those barnacles from higher up the shore have less tissue per unit volume of shell (external) than those from lower down. The approximate mean values for the year, in terms of mgm. of dried tissue per mm^3. of external shell volume were 0·130, 0·083 and 0·080 on B.1, B.2 and B.3 respectively. It is to be expected that the barnacles most exposed to dessication from solar radiation, will require the thickest shells for protection. This has already been shown in the case of limpets (Orton, 1933).

Changes in the Gonads with Season and Age.

The general anatomy of the barnacle has been described by Darwin (1851), Gruvel (1905), Krüger (1927) and others. Spence-Bate (1869) has described the process of impregnation, and Hoek (1876) and Runnström (1925) describe the larval stages and process of metamorphosis. The larvæ are normally liberated into the sea as Stage I nauplii, although Runnström records a doubtful case where they may perhaps have been retained and not liberated until the cypris stage.

According to Runnström the barnacles at Herdla near Bergen begin to ripen their ova at the end of October or beginning of November. The embryos develop in the mantle cavity during the winter and are liberated in maximum numbers about the middle of March. At the end of March and beginning of April they begin to settle as Cypris on the shore. Elmhirst (1922), describing conditions at Millport in the Clyde, gives the hatching season as January to April, with a maximum in March and April. Johnstone, Scott and Chadwick (1924), summarising fourteen years' plankton investigations in Port Erin Bay, show that a few Balanus nauplii are present throughout the year, but that the greatest numbers occur from February to April.* There is an interval between the maxima for the nauplius and the cypris stages of nearly two months, and where the nauplii were taken in ten thousands, the cypris were taken only in tens. The difference was no doubt due in part to mortality and to dispersal of the larvæ, and in part also to the difference in time of duration of the two stages. The monthly mean figures given by them are shown below.†

Month.	Nauplii.	Cypris.
December . . .	2	–
January . . .	404	–
February . . .	5322	–
March	35224	–
April	11021	40
May	585	70
June	13	5
July	–	–
August . . .	1	–

In 1932 we observed the first settled cypris larvæ on the rocks at Port Erin on April 26th, in 1933 on April 25th, and in 1934 on the same date. This shows surprisingly little variation in successive years. Hatton and

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* The species was not identified, but *B. balanoides* is far the most abundant species in the neighbourhood.

† These are the mean numbers for the half of the combined hauls of a No. 19 and a No. 20 gauge net, 35 cm. in diameter, towed for a distance of 800 metres.

Fischer-Piette (1932) record the first settled spat near St. Malo in 1930 between March 29th and April 2nd, the subsequent settlement continuing for about six weeks. In 1931 the first spat settled between February 15th and March 4th, and the settlement lasted for about three months. Grave (1933) gives the date of metamorphosis at Woods Hole, Massachusetts, as February 15th to March 15th.

The material used in the present work on the condition of the gonads was collected at intervals throughout the year from the three levels at Port Erin, and also from the two extra patches of barnacles of known age, B.4 and B.5. From three to ten individuals of each recognisable year-group, from each level, were decalcified and sectioned, and the following is a summary of the results obtained.

B.1 (and B.4). *Low level.*	B.2 (and B.5). *Intermediate level.*	B.3. *High level.*
March 17th, 1933.		
All barnacles contained advanced larvæ in the mantle cavity.	All but the first-year specimens contained advanced larvæ in the mantle cavity. First-year specimens showed no gonad development.	First - year specimens showed no gonad development. Older ones had mantle cavities containing large numbers of advanced larvæ, except some senile individuals (see p. 270).
April 28th, 1933.		
Spawning of larvæ entirely over. Large specimens contained developing ova and a medium-sized ovary. Even some first-year barnacles showed ova. No proliferation of testicular cæcæ.	Conditions similar to B.1, except for the absence of developing gonads in first-year individuals.	Conditions similar to B.2.
June 26th, 1933.		
No proliferation of testicular cæcæ in any specimens. First-year specimens with small ova and ovaries. Older barnacles with larger ova and ovaries.	First-year barnacles with no trace of gonads. Older ones as on B.1.	Conditions as on B.2.
September 18th, 1933.		
First-year barnacles with small testicular cæcæ containing early spermatogenesis stages. Ovaries small, with small developing ova. Older individuals with large testicular cæcæ, and more advanced sperm, some apparently ripe. No spermatozoa yet in vesiculæ seminales. Ovaries as in first-year specimens, but larger and more mature.	First-year barnacles with no trace of gonads. Older ones as on B.1.	Conditions as on B.2.
November 1st, 1933.		
Ovaries of all ages full of large ova. Abundant sperm in both testicular cæcæ and vesiculæ seminales, though spermatogenesis stages still present in the former.	First-year individuals with no gonads. Older specimens as on B.1.	Conditions as on B.2, but a few individuals had shed their ova into the mantle cavity where they had been fertilised. Some senile specimens with few or no ova in the ovary.

Two sets of samples also were collected from the more wave-exposed locality outside Bradda Head, and the following is a summary of the results obtained from them.

September 5th, 1933.

Level—5′ 5″ (slightly above low water of ordinary neap tides).

First-year individuals with no proliferation of the testicular cæcæ, but the vesiculæ seminales were large. Ovaries containing small developing ova.

Second-year and older individuals with slight proliferation of the testicular cæcæ and early spermatogenesis stages, but no ripe sperm. Ovaries larger and more mature than in the younger specimens.

Level—1′ 2″ (slightly below mean sea level).

First-year specimens with no trace of gonads. Older ones with large testicular cæcæ containing some apparently mature sperm. Ovaries large and containing large ova.

Level. +6′ 2″ (high water of ordinary neap tides).

Conditions as at —1′ 2″, except that no mature sperm were seen.

Level. +7′ 2″.

Conditions as at a foot lower.

November 17th, 1933.

Level. —5′ 5″.

Gonads ripe in all ages. Vesiculæ seminales full or ripe sperm. Ovaries smaller in first year than in older specimens, but in both cases full of mature ova. At this level no specimens were found which had shed their ova.

Level. +7′ 6″.

All mature individuals (more than one year old) had shed their genital products and contained early developing embryos, except certain senile individuals, of which there was a large proportion among the biggest specimens.

These results may be summarised as follows. At all levels the ovaries develop and mature considerably earlier than the testes, and are in fact well developed while the barnacle is still carrying in its mantle cavity the larvæ of the previous brood. The testicular cæcæ begin to proliferate and show early spermatogenesis stages in the autumn, and ripe spermatozoa are to be found by November. In this month shedding of the ova and impregnation take place, the barnacles from the highest level on the shore being most advanced, and shedding their genital products first. Liberation of the nauplii into the sea takes place from February onwards, with a maximum in March, the liberation also commencing slightly earlier in those animals which are furthest up the shore.

At these localities (Port Erin and Bradda) the first-year barnacles do not develop gonads at levels on the shore above about half-tide level. Below this point maturation occurs in the first year, and development follows much the same course as it does in the second year at higher levels, except for being slightly slower in the earlier stages. The age of maturity was checked on the patches B.4 and B.5 at Port Erin. On B.5 (+2·74 feet O.D.) which was completely scraped early in 1932 in time to receive the spat-fall of that year, no larvæ were found in any of the 1932 brood when these were examined in the spring of 1933. On B.4 on the other hand (—0·75 feet O.D.), which was cleared at the same time, all individuals showed larvæ in the mantle cavity the following spring.

Runnström records that at Herdla the majority of the first-year barnacles were without gonads, but that a few small individuals, apparently in their first year, were found to contain nauplii. He does not state the level at which these were taken, but it looks as though they were comparable with the early-maturing B.1 type at Port Erin.

In the above account of the conditions of the gonads, some individuals are recorded as senile. The cause of this condition is not known. Such individuals have been found only in the extreme upper limit of the barnacle zone (B.3). The condition is not limited to isolated barnacles, being equally common in members of crowded communities. It is found chiefly in the larger individuals, becoming more frequent with increasing size, and was never seen in very small specimens. In fact it appears to be a condition which is subsequent on at least one season of normal spawning, as distinct from a type of permanent sterility which will be described in a later paper. Progressive stages in the onset of this senility may be found (Fig. 2), from those barnacles which produce a normal number of larvæ, through those which produce a few only, to those which produce none at all. In the latter the appearance of the ovary when the animal is removed from the rock, is large and swollen, and yellow in colour and quite distinct from the normal condition. In section, those with a small larval content are apparently normal, except that in some cases they seem to contain an abnormally high proportion of relict ova. Some of those individuals which have failed to produce any larvæ at all, are found to have produced both ova and sperm, but have failed to shed either. In more extreme cases the ovary is reduced in size, and seems to have produced few or no ova, and in some of these the amount of sperm in the vesiculæ seminales is also less than normal. Finally, in one of the most pronounced examples examined the testicular cæcæ were in a very retarded condition and contained only early spermatogenesis stages at a time when they should have been filled with ripe spermatozoa.

The reason for this sterility is not apparent. It may possibly be due to some form of parasitic castration, since many barnacles are found to contain one or more unidentified cysts about 200μ in diameter. Lebour (1911) has recorded *Cercaria balani* encysted in this species, and *Gregarina* cysts are also known in various barnacles (Trégouboff, 1912; Kamm, 1922). In addition an Epicarid Isopod, *Hemioniscus balani* (Sp. Bate) is known to infect *Balanus balanoides* in some localities, but only a single specimen was found in the whole of the work at Port Erin.

OUTPUT OF LARVÆ.

For the determination of the larval output, material was collected in February, 1933, from the three levels at Port Erin at a time when the larvæ were well developed, but when no spawning had taken place. A series of specimens was chosen, covering the full range of sizes at each level, and the size (length, breadth and height) of each individual was measured. The mass of larvæ was then removed from the mantle cavity of each, and teased apart under a dissecting microscope, and either the whole or a part of each was counted on a ruled slide. The results obtained are given in Table VI, and in Figure 3 are shown the superimposed outlines of the scatters for the three levels.

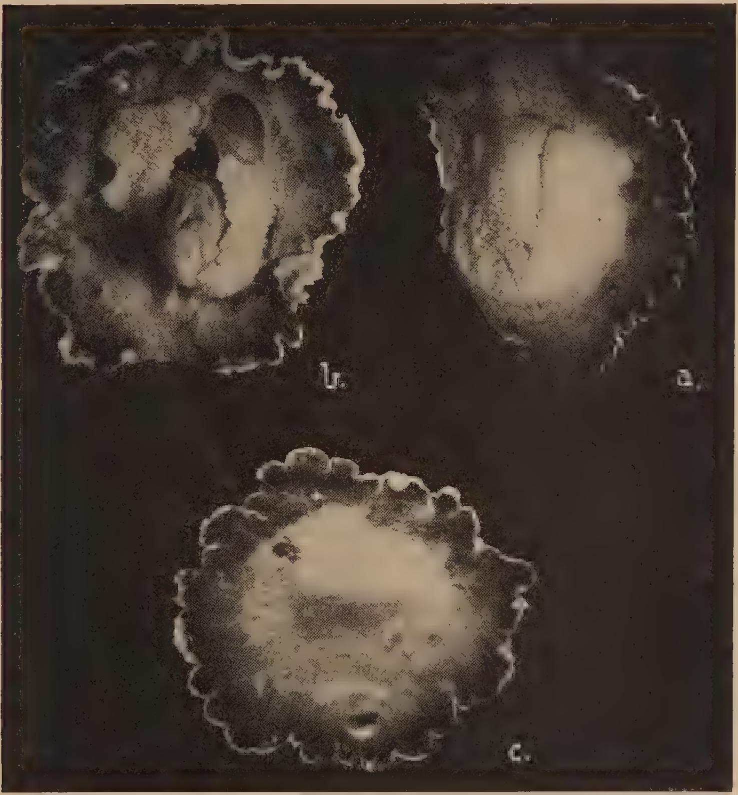

FIG. 2.—*B. balanoides* from the top zone at Port Erin, seen from below. (*a*) A normal individual with full complement of nauplii in the mantle cavity. (*b*) Early condition of senility with reduced number of nauplii. (*c*) Advanced stage of senility with no nauplii, and swollen, fatty ovary. × 4.

At the lowest level (B.1) breeding takes place a year earlier than at either of the other two levels, and this, together with the smaller growth-rate at B.1, allows larvæ to be found in much smaller specimens there than elsewhere. Otherwise the three levels are similar except for the larger barnacles on B.3. Here, owing to the appearance of senile individuals among the larger barnacles, the lower limits of the scatter drop to zero above a size of about 100 mm^3. The upper limits on all three levels are similar. As an example of the wide range of naupliar content found in the larger specimens on B.3, four specimens with sizes of 209, 210, 211 and 216 mm^3. respectively had naupliar contents of 0, 5890, 13110 and 2043.

Figure 4 shows the larval output of average individuals of successive year groups at the three levels, calculated from the growth stages previously obtained for that locality (Moore, 1934). The low level, B.1 barnacles, by reason of their earlier spawning, yield, from the point of view of the plankton, a quicker return than do those from higher levels, but their size in their first year is so small that their larval output is almost negligible, and few of them survive to spawn a second time. In their first spawning year the output of B.2 and B.3 is very similar, lying between 1500 and 2000 larvæ per individual, but in subsequent years the proportion of senile non-spawning individuals on B.3 reduces the average output on B.3 slightly below that for barnacles of the same age on B.2,

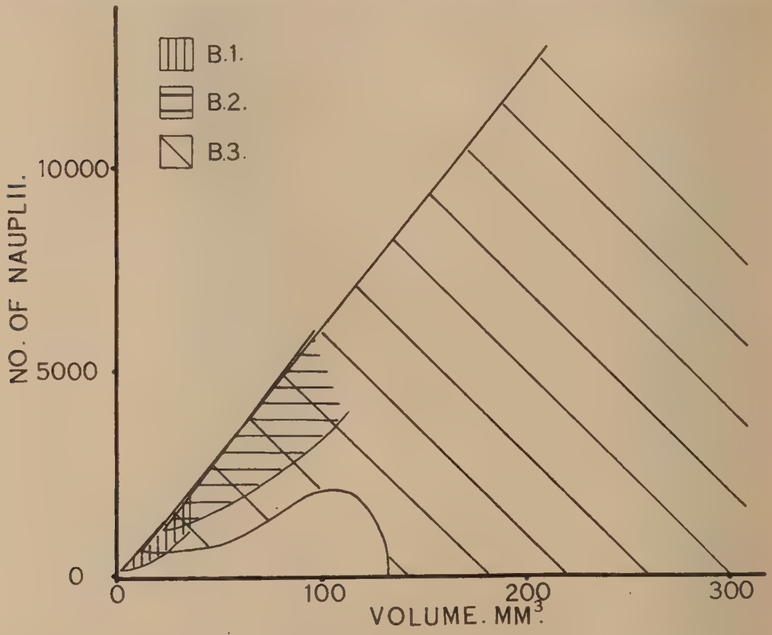

FIG. 3.—Relation of naupliar content to size in *B. balanoides* at Port Erin at low-level (B.1), intermediate- (B.2) and high-level (B.3).

despite the slightly greater size of the former. On the other hand very few B.2 barnacles survive to spawn more than twice, whereas the B.3 type may apparently live and spawn for a number of years.

In order to obtain an estimate of the weight of a nauplius, a number of barnacles were taken from the shore in March, 1934, just prior to the time of spawning. After removal from the rocks the barnacles were stirred up in sea-water and the larvæ set free. These were then decanted into one end of a long glass vessel which was illuminated only from the other end. The liberated larvæ swam towards the light, so that a pure suspension of them could be siphoned off from that end of the vessel. The number of larvæ so obtained was estimated as 3,480,000 from a series of counts of aliquot portions. The larvæ were then collected on a weighed filter paper, washed by drawing a small quantity of distilled water over them, and dried to a constant weight in a boiling-water oven. From these the average weight of one nauplius was estimated as $7{\cdot}5 \times 10^{-4}$ mgm.

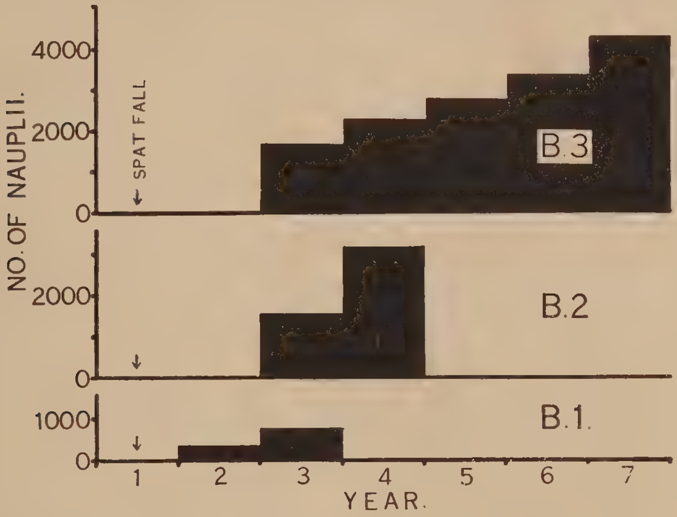

FIG. 4.—Mean naupliar output in successive years at three levels at Port Erin.

SUMMARY.

1. The relation between the dry weight of the decalcified barnacle and its shell volume has been determined in its relation to age, season and tidal level, at Port Erin, with the following results: (*a*) In immature barnacles, tissue growth continues throughout the year, but is most rapid in the spring and autumn. (*b*) In mature barnacles which produce a considerable

amount of larvæ there is a heavy drop in tissue weight during the summer period of high temperature, and another slighter drop during the winter, the latter being apparently associated with the presence of developing larvæ in the mantle cavity.

2. Gonad samples were examined seasonally. At low levels on the shore the barnacles mature in their first year. Above this level they do not commence to mature until over a year old. The sequence of changes in the gonads is described. A condition of senility is found in many of the largest high-water barnacles.

3. The naupliar content was estimated in relation to size and tidal level, counts of up to 13,000 larvæ per individual being obtained. The dry weight of a fully developed nauplius was determined to be $7{\cdot}5 \times 10^{-4}$ mgm.

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TABLE I.

Observed Mean Tissue Weights and Mean Shell Volumes on August 25th, 1932, at Port Erin.

Weights in mgm.; volumes in mm³. (see p. 263).

B.1.

vol.	weight.	year group.
17·5	1·16	1931 or earlier

B.2.

vol.	weight.	year group.
7·64	0·32	1932
10·3	0·29	
32·3	1·12	
42·0	4·6	1931 or earlier
67·6	7·4	
108	10·4	

B.3.

vol.	weight.	year group.
52·4	4·08	1931 or earlier
75·5	5·95	
109	8·37	
155	12·5	
213	17·2	
283	22·4	

TABLE II.

Observed Mean Tissue Weights and Mean Shell Volumes on October 25th, 1932, at Port Erin.

Weights in mgm.; volumes in mm³.

B.1.

vol.	weight.	year group.
3·13	0·30	1932
10·13	0·83	
19·26	1·45	1931 or earlier

B.2.

vol.	weight.	year group.
7·66	0·53	1932
14·8	0·81	
26·5	1·28	
32·1	2·00	1931 or earlier
42·4	4·0	
51·8	5·91	
69·1	6·92	
74·3	6·86	
93·1	11·00	
97·25	11·00	
134·5	9·0	
136·5	11·85	

B.3.

vol.	weight.	year group.
7·81	0·41	1932
21·71	0·80	
24·04	0·88	
25·50	2·30	1931 or earlier
51·22	5·17	
73·16	9·00	
152·9	13·8	

TABLE III.

OBSERVED MEAN TISSUE WEIGHTS AND MEAN SHELL VOLUMES ON JANUARY 25TH, 1933, AT PORT ERIN.

Weights in mgm.; volumes in mm³.

B.1.

vol.	weight.	year group.
3·63	0·29	1932
5·38	0·61	1931 or earlier
9·16	0·88	
14·4	1·54	
30·6	2·85	

B.2.

vol.	weight.	year group.
4·95	0·40	1932
10·8	0·92	
20·3	0·81	
25·6	1·39	
28·6	2·25	1931 or earlier
56·8	4·00	
76·3	5·80	
89·8	7·30	

B.3.

vol.	weight.	year group.
10·1	0·46	1932
20·7	1·10	
30·1	1·38	
33·1	2·96	1931 or earlier
68·2	5·22	
104	8·42	
217	23·4	

TABLE IV.

OBSERVED MEAN TISSUE WEIGHTS AND MEAN SHELL VOLUMES ON APRIL 26TH, 1933, AT PORT ERIN.

Weights in mgm.; volumes in mm³.

B.1.

vol.	weight.	year group.
6·97	1·48	?
15·5	2·92	
28·7	4·35	

B.2.

vol.	weight.	year group.
8·15	0·83	1932
14·3	1·32	
24·9	2·23	
29·8	3·00	
74·0	5·64	1931 or earlier.
94·2	7·86	

B.3.

vol.	weight.	year group.
7·68	1·28	1932
17·4	1·82	
33·4	3·46	
67·9	4·33	1931 or earlier
94·3	6·00	
206	16·5	

TABLE V.

OBSERVED MEAN TISSUE WEIGHTS AND MEAN SHELL VOLUMES ON JUNE 14TH, 1933.

Weights in mgm.; volumes in mm³.

B.1.

vol.	weight.	year group.
1·75	0·17	1933
9·85	2·25	1932 or earlier
20·3	3·73	

B.2.

vol.	weight.	year group.
0·77	0·068	1933
19·7	2·12	1932 or earlier
35·7	3·72	
50·1	4·82	
96·6	8·00	

B.3.

vol.	weight.	year group.
0·75	0·070	1933
25·2	2·45	1932 or earlier
41·3	3·26	
45·2	3·45	
48·2	5·26	
52·0	6·12	
105	8·06	
158	11·2	
268	19·8	

TABLE VI.

INDIVIDUAL NAUPLIAR CONTENTS OF *Balanus balanoides* AT PORT ERIN, FEBRUARY, 1933.

B.1.		B.2.		B.3.		B.3.	
Vol. in mm^3.	No. of Nauplii.	Vol. in mm^3.	No. of Nauplii.	Vol. in mm^3.	No. of Nauplii.	Vol. in mm^3.	No. of Nauplii.
3·52	218	24·9	1160	29·7	757	163	3970
4·62	226	31·0	1190	38·5	662	177	8438
6·22	251	34·8	1240	43·6	843	195	none
6·68	173	46·8	2290	46·0	2230	195	3020
6·68	174	59·6	1830	49·7	2930	205	7030
7·47	173	64·5	2760	56·5	1250	209	9460
8·74	419	66·8	3440	68·0	2460	209	none
9·28	173	67·0	4040	68·8	2230	210	5890
9·86	413	67·6	2230	77·1	3433	211	13110
10·5	420	72·2	2200	77·4	1710	216	2043
11·8	431	72·5	4400	86·0	2250	217	5327
12·5	532	85·9	2610	93·0	2190	232	9590
12·5	386	101	5210	93·1	2350	234	5020
12·5	328	102	6070	97·4	3700	235	none
13·9	507	110	4230	122	5140	241	4210
13·9	611	112	5600	131	none	243	none
15·5	280	113	3980	135	none	250	7360
15·5	401	115	5850	141	5480	254	10770
16·4	404			161	4770	266	6090
18·1	543			163	none	301	6466
18·1	725						
24·1	1372						
25·2	623						
35·4	1162						
39·8	1022						

The Biology of *Balanus balanoides*. IV. Relation to Environmental Factors.

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Marine Biological Laboratory, Plymouth.

With 11 Figures in the Text.

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GENERAL.

THE most detailed work on the distribution of *Balanus balanoides* and its relation to its habitat, so far as European seas are concerned, is that of Fischer-Piette and of Hatton. In Hatton and Fischer-Piette (1932) an account is given of four localities of progressive degrees of wave-exposure, in the neighbourhood of St. Malo, together with the density of population of the barnacles at four different levels at each locality, and their rate of growth and mortality. In Fischer-Piette (1928 and 1932) a further account is given of the distribution of this species along the French coasts of the Channel, and the variations in its zonation and abundance in so far as these can be related to environmental conditions. In Fischer-Piette (1929) a detailed description is given of the distribution of this and other species up the estuary of la Rance, in relation to the wide range of physical and chemical conditions found there, from which it has been possible to give the limiting values for some of these factors. Finally, in Fischer-Piette (1934), the account of the distribution of this species along the Channel coasts is extended to include the south coast of England, and the north coast of Cornwall.

In earlier papers of the present series (Moore, 1934, 1935) an account has been given of the growth of the shell and the seasonal changes in the soft parts of *B. balanoides* growing at various tidal levels in Port Erin Bay, in the Isle of Man, this locality being typical of a fairly exposed coast. The present paper relates the growth, maturity, etc., of the barnacles to certain of the environmental factors, and as one of the chief of these, after tidal level, is the degree of exposure to wave-action, an attempt has been made to give some numerical value to this factor.

After discussion with Mr. J. R. Bruce, the following factor has been chosen as probably representing the closest approximation permissible in the present state of our knowledge. In the absence of a direct measure of the force of incident waves, a theoretical value might be arrived at from a knowledge of the amount and force of the winds incident on the locality in question, and the forces of waves which they would produce. The angular aperture of the locality may be determined, and in addition the number of days in the year with winds of measured direction and force are frequently available. Further, the wave-raising power of a given wind is known, but two factors are at present undetermined. These are the exact effect of a shallow bottom near the shore, and the relation between "fetch," or the distance over which the wind has acted on the water, and the size of the wave produced when the wind is less than gale force and the distance is less than the amount necessary to produce the maximum wave possible for the wind in question. Lacking the full data required for a calculation of the desired factor, we have chosen a factor for wave-action which is defined as the number of days per hundred days in which any wind blows into the exposed aperture of the locality in question, this opening being the seawards aperture measured at a distance of half a mile. Thus, if the year's wind were uniformly distributed, a locality open through 180° would have an exposure factor of 50.

Such a factor is admittedly far from perfect in many respects, but it seems adequate for comparing a series of localities such as those used in the Isle of Man. And it is to be hoped that in the future a more perfect measure may be produced.

Fischer-Piette (1932) chose four degrees of wave-exposure which he defined as follows :—

Très battu.

Peu battu, mais encore dépourvu de Fucacées.

Abrité et couvert de Fucacées.
Très abrité.

The species and abundance of the Fucaceæ present is a useful guide to exposure, but clearly some more physical measure is desirable.

The four localities worked in the Isle of Man are as follows :—

A. *Inner Pier, Port St. Mary.* Exposure factor 0.

Situated on the vertical face of the inner side of the pier, about 25 feet from the seaward end, and having its lowest zone about 7 feet above a bottom of mud and gravel. The surface of attachment is limestone. The locality faces west and is not exposed at all to the open sea.

B. *Alfred Pier, Port St. Mary.* Exposure factor 8.

Situated on the vertical face of the inner side of the Alfred Pier, about 800 feet from the seaward end. The surface of attachment is dressed limestone blocks faced with cement except where this has flaked off in the lowest zone. The bottom, two to ten feet below the lowest zone, is rocks and coarse shingle. The locality faces north-west, and has a slight exposure over a distance of more than half a mile of water, though not to really open sea.

C. *Dub Reef, Port Erin.* Exposure factor 30.

This is the locality where most of the previous work has been done (Moore, 1934, etc.). It is the vertical face of a gulley in the rocks on the east side of Port Erin Bay. The surface faces roughly south, and has a considerable lateral exposure to the west to the open sea. The substratum is Manx slate, and the bottom, below the barnacles, is rocks.

D. *Outside Bradda Head.* Exposure factor 55.

This was the most wave-exposed locality available. It is completely open to the sea from NNE to SSW, and faces west. The substratum is Manx slate, and the bottom shingle and rocks. There is an abrasion zone of clean rock surface for about a metre above the shingle, so care had to be taken to avoid this in choosing a traverse.

Levels throughout this paper are referred to ordnance mean sea level for the Isle of Man. In the case of Port Erin and the two Port St. Mary localities the levels of the barnacle patches were referred by tape to a datum kindly fixed for me by Mr. J. R. Bruce. This was not possible outside Bradda, and the necessary measurements were made from the level of the water on a very calm day, simultaneous measurements being made on a tide staff in Port Erin Bay. High water of mean neap tides at Port Erin is approximately four feet above mean sea level, and high water of mean and extreme spring tides respectively eight feet six inches, and ten feet above.

The material was obtained from a traverse down the shore in each locality, worked in June–July, 1933, with additional samples taken at other times for details of the condition of the gonads, etc. Samples were taken at successive levels, and the various year groups were distinguished as far as possible (Parke and Moore, 1935). A selection from these was then sorted into size groups, decalcified, dried and weighed (as in Moore, 1935, p. 264), and the results obtained are given in Tables I to IV.

Relation of Vertical Distribution to Wave-Exposure.

The extreme upper and lower limits of distribution of barnacles on the open rock surface are shown in Figure 1, plotted against the wave-exposure of the localities. Young spat can sometimes establish themselves beyond the limits at which adults are found, but the presence of adults may be taken as defining the limits within which the species can establish itself. In the case of Port Erin, in June, 1933, for example, no adults were found below a level of —6′ 2″, although there were spat of that year's brood a foot below that level.

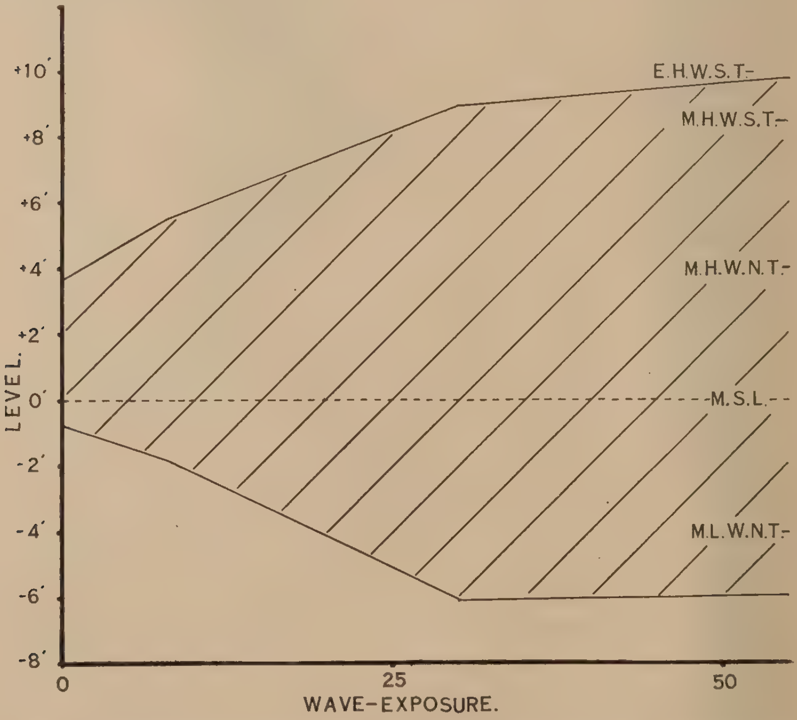


Fig. 1.—The variation in the upper and lower limits of distribution of *B. balanoides* with varying degree of wave-exposure. H.W.=High water; L.W.=Low water; M.S.L.= Mean sea level; M=mean; E=equinoctial; S.T.=Spring tide; N.T.=Neap tide.

The upper limit at the very sheltered locality at Port St. Mary inner pier is almost exactly at high water of mean neap tides, and Fischer-Piette (1929) states that this upper limit is adhered to all along the Channel coasts. With increasing exposure to wave-action, the upper limit rises, until outside Bradda it is almost at high water of extreme spring tides, but it must be remembered that these levels are absolute, and do not take into account the extent of the splash-zone (Orton, 1929, p. 279), which would probably be sufficient alone to account for this added six feet. However, in calm weather, these barnacles must have to exist for days at a time without being touched by the water.

The lower limit of distribution drops similarly with increasing wave-exposure, from just below mean sea level at Port St. Mary inner pier to half-way between mean low water neaps and mean low water springs at Port Erin. The fact that there is no further drop outside Bradda suggests that this is the lowest limit at which they can establish themselves. The abnormally good spatfall of 1933 populated the rocks at Port Erin down to —7′ 8″, but no mature animals were found to have survived below —6′ 2″.

The connexion between the upper limit and high water of neap tides is obvious, suggesting that, except for short periods, this species require to be reached by the water every day. And it may be noted that those barnacles which live at the extreme top limit are few in number and thick shelled. The reason for the lower limit is, however, not clear. If we assume that for an animal which requires the intertidal conditions of contact with both air and water each day the splash zone will not only raise the upper limit of high water, but also drop the level of low water, since the wash of the waves will carry air to a level below actual low water mark, then the observed drop in the lower limit for Balanus at increasing wave-exposures may be to some extent accounted for. This species definitely requires these intertidal conditions since it is not normally found below the level of low water, and since, except in the type of locality found outside Bradda Head the species thrives best as an adult at the top of its distribution. At any rate some powerful limiting factor must be operative since outside Bradda the lower limit is so sharply defined, and yet immediately above it is the zone of earliest maturation, and of the most rapid growth rate which has been found in the neighbourhood. Further it seems probable that a different factor is responsible for raising the lower limit in more sheltered localities, where low water conditions are definitely disadvantageous to all but the youngest barnacles (see p. 288).

RELATION OF DENSITY OF POPULATION TO WAVE-EXPOSURE.

That wave-exposure situations are advantageous to the growth of this species has already been shown (Fischer-Piette, 1929). Numbers of individuals are an unsuitable measure of quantity in comparing different barnacle communities, since in tightly packed areas the largest numbers will be found where the barnacles are smallest, and the largest numbers of all will of course be found in recently denuded rocks which have been heavily recolonised by spat. A better figure to use is the weight of tissue per unit area. Taking all ages of barnacles together, the maximum weights found at any level were, in order of ascending wave-exposure, 1·4, 8, 24 and 178 mgm. per sq. metre.

Fischer-Piette has further stated (1929) that the advantageous effect of wave-action on the growth of barnacles may be reproduced by a current of water. This was confirmed by observations in the Clyde and at Plymouth, and also in material collected for me at Lough Ine, in Ireland, by Dr. M. W. Parke. This latter material consisted of samples taken from approximately the same tidal level at three localities. The first of these was inside the lough where there was very little wave-action and practically no current. The second was in the rapids which connect the lough with the open sea, and in which there is little true wave-action, but a very strong flow of water. The third was in the open sea on the very wave-beaten coast outside the lough. The barnacles from inside the lough were small and those from the open sea much larger, while those from the current-swept region of the rapids were definitely of the large outside type. A further effect of currents is discussed later (see p. 295).

MODIFYING INFLUENCE OF WAVE-EXPOSURE ON THE EFFECT OF LEVEL ON GROWTH RATE, BODY WEIGHT, DENSITY OF POPULATION, ETC.

The simplest condition with regard to the two factors of level and wave-exposure is found in the newly settled spat. The samples taken in June–July clearly show that the largest first-year barnacles, and consequently those which have grown most rapidly (because settlement occurs simultaneously at all levels), are those which are living at low water, and further that growth has been progressively less towards high water (Fig. 2). This generalisation holds good for all degrees of wave-exposure, but the general rate of growth is greatest in the most exposed situations. Among the older animals, however, conditions are more complicated (Fig. 3). In the very exposed situations outside Bradda the same condition of greatest growth rate at low water holds good for the second- and third-year barnacles also; but at all the more sheltered stations the optimum level for growth moves steadily up the shore with advancing age, so that the oldest barnacles are growing fastest at the top of their distribution. This is also shown in Moore (1934), Figure 3, where the mid-zone barnacles B.2, were considerably larger in their first year than the corresponding top-zone ones on B.3, but were slightly smaller in their second and subsequent years. Figure 4 of the present paper shows typical areas of rock at Bradda and Port St. Mary, and illustrates the population

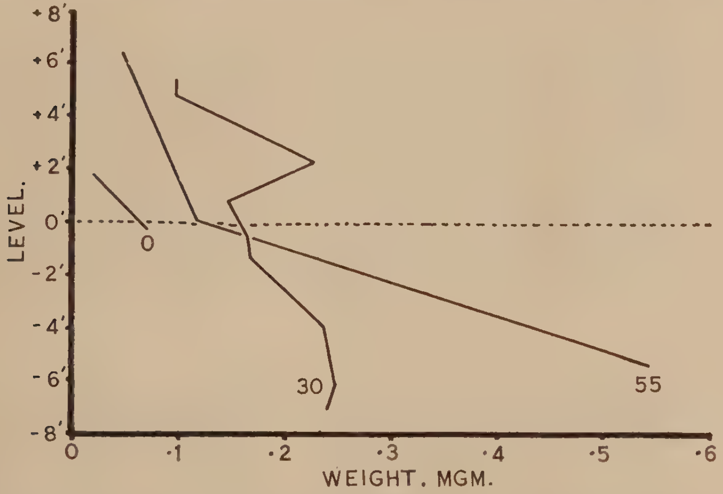


Fig. 2.—Variation in the mean size (tissue weight) of the population with tidal level at different degrees of wave-exposure (indicated by figures alongside curves). First-year individuals only.

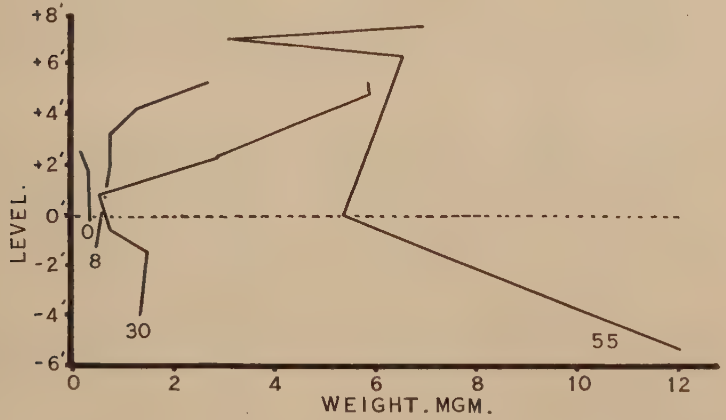
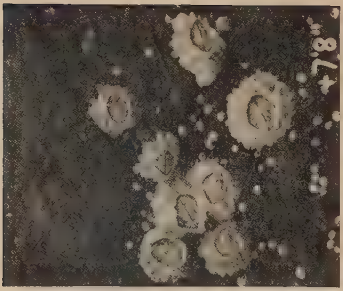


Fig. 3.—Variation in the mean size (tissue weight) of the population with tidal level at different degrees of wave-exposure (indicate by figures alongside curves). Individuals of two years old and over.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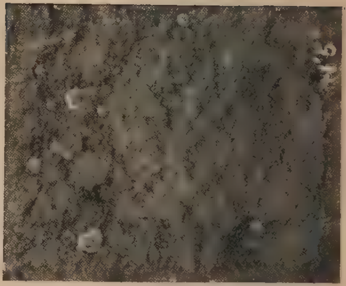
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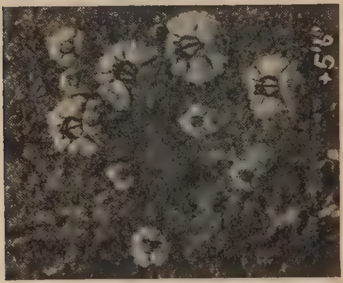
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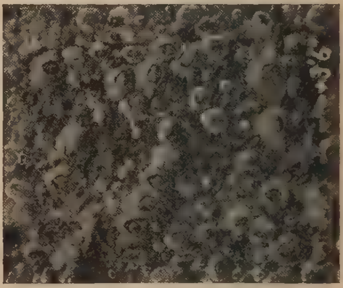
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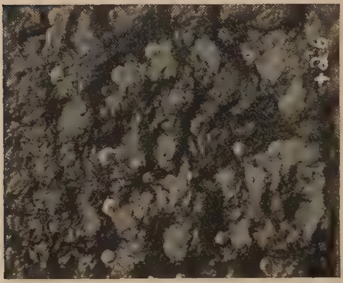
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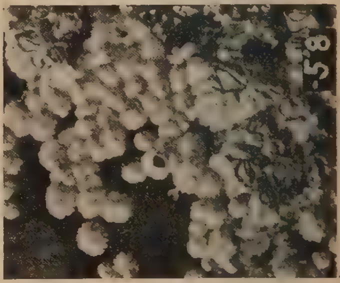
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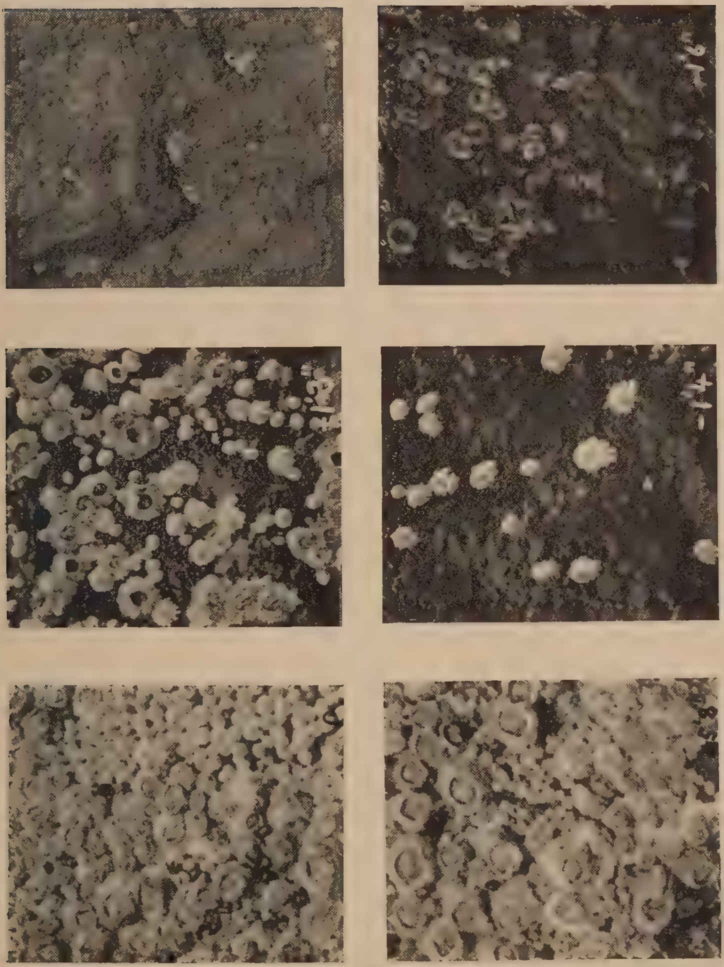

Inner Pier, Port St. Mary.

Alfred Pier, Port St. Mary.

Outside Bradda Head.

FIG. 4.—Typical areas of rock from the two Port St. Mary localities and from outside Bradda Head, photographed in July, 1933, all life-size.

density, and the size attained by first-year and older barnacles in relation to tidal level and wave-exposure. Fischer-Piette (1932) also has recorded the more rapid growth of the newly settled spat at low water and in exposed situations, but he does not give data on the comparative growth of the older barnacles.

The advantage of the low water conditions for the young barnacles is understandable, since they are comparatively thin-shelled and little able to withstand dessication. All ages also will be able to feed for a longer period at low water, and will be able to filter the greatest amount of water where this water is being moved by waves. But it would appear that either there is a harmful factor present in the water in more sheltered situations which tends to retard the growth of the older barnacles, but not of the spat, and perhaps thereby raises the lowest limit at which they can survive (see p. 283), or else that there is a beneficial factor in a condition of exposure to the air. Such a factor would be counterbalanced in the young barnacles by their difficulty in withstanding dessication. It is true that they are less liable to the attacks of enemies such as Purpura at higher levels, but this would affect their death rate and not their rate of growth. And it must be remembered that the barnacle is a plankton-feeding animal which is dependent on the period when it is covered by the water for obtaining its food.

In those localities where the supply of food is more than usually abundant as outside Bradda, where an extra large quantity of water is brought within reach of the barnacle, and in the quiet waters of the River Tamar at Plymouth, where the water is very rich in suspended food matter, this factor clearly outweighs all others, and growth is greatest at low water. But where such strongly beneficial low water conditions are not present a second factor comes into play, and of the two possibilities suggested above, that of the harmful factor in the water seems to be the more likely.

It has already been shown (Moore, 1935, 1) that the ratio of tissue weight to shell volume varies with season, age and tidal level. The results of the present survey bear out, so far as they go, those obtained at Port Erin that the relative weight of tissue is in general greatest at low water, and is greater in mature than in immature individuals.

The Effect of Level on the Maturation of the Gonads, and the Modifying Influence of Wave-Exposure on This.

In Moore (1935) it was shown that, at Port Erin, maturation of the gonads occurs in the first year in barnacles living below half-tide mark, but not until the second year in animals from above this level. In February, 1934, a survey was made of the conditions of the gonads at the four Isle of Man localities at a time when all spawning barnacles contained well-developed larvæ in the mantle cavity.

In the upper levels at Port Erin a non-spawning type of barnacle was found which was described as senile (Moore, 1935, p. 270). At the two Port St. Mary localities specimens were found of another non-spawning type in which gonads had failed to develop at any age, as distinct from the senile barnacles which had ceased to develop genital products after a period of normal spawning. In some zones it is normal for there to be one vegetative year before the gonads mature, and this condition of sterility appears to be an extension of this vegetative period due to adverse conditions. Fischer-Piette (1934) records that at the Scilly Isles, at the extreme western limit of their range in Great Britain, the Balanus were not producing any larvæ. The sterile individuals at Port St. Mary could be readily distinguished from the senile ones by the condition of the basal membrane. This was thin and dark in the sterile barnacles as it is in young

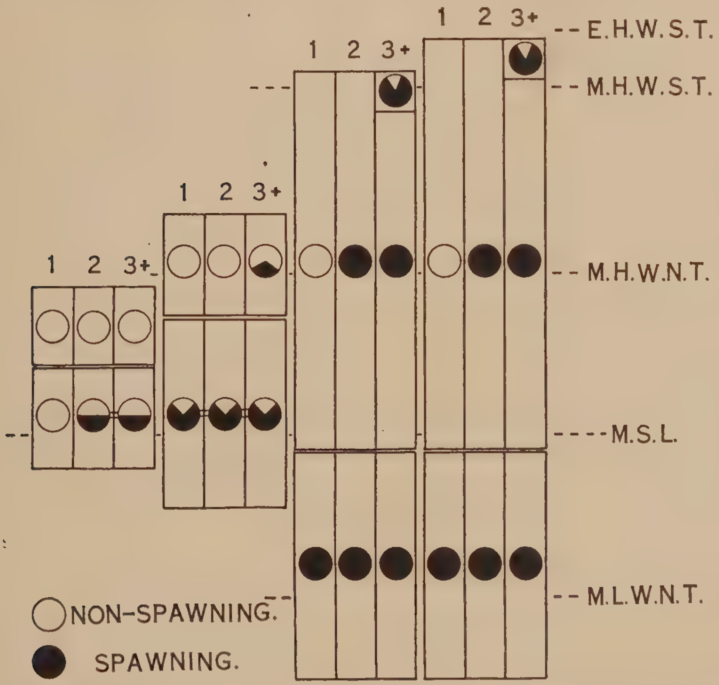

FIG. 5.—Diagram of the condition of maturity of the gonads in relation to age and tidal level (age in years is indicated by the figures at the top), at Port St. Mary inner pier (left), Port St. Mary Alfred pier, Port Erin and outside Bradda Head (right), in February, 1934.

immature individuals, while in the senile ones it was yellow and swollen with degenerating relict ova.

At Port Erin and Bradda conditions were very similar (Fig. 5). Below about half-tide level all the barnacles matured in their first year, and liberated larvæ when a year old (counted from the time when they were spawned). Above this level maturation did not occur until a year later, but occurred then in all individuals. In the third year a proportion of senile individuals began to appear, though no definite figure can be given to their frequency, since the condition is progressive.

At the Alfred Pier, Port St. Mary, in the lower zone, about 75% of the barnacles were mature, the rest apparently not maturing. Unfortunately it was not possible to separate the year groups here with certainty, but it appeared probable that there were present both mature and immature barnacles of all ages. In the upper levels, where the year groups were more readily distinguishable, no mature barnacles were found in the first- or second-year groups, and in the third-year group only about 30% were mature.

Finally, in the very sheltered situation of the inner pier, Port St. Mary, no mature individuals at all were found in the upper levels, and in the lower zone only about 50% of the two-year-old and older barnacles were mature. No mature first-year barnacles were found here.

The effect of increased exposure to wave-action is therefore to accelerate the onset of sexual maturity, and this always occurs earlier at low levels on the shore than it does higher up. A full series may be obtained of barnacles maturing in their first, second or third years or not at all.

The Effect of Temperature, Salinity, Oxygen Concentration, pH, and Sediment.

Observations on the environmental conditions are unfortunately few. A barnacle living between tide marks is exposed to two entirely different types of conditions according to whether it is immersed or exposed. When exposed to the air, the barnacle's shell is closed, and the barnacle is extremely resistant to adverse outside conditions. Also, if immersed in water which is in any way harmful, the shell can be closed and the animal protected for a considerable period. It must be able to avoid desiccation for some time when left by the tide, probably on some occasions for as much as a week in extreme instances such as outside Bradda. Cole (1932) records an experiment in which a group of *B. tintinabulum* were removed from the sea which was at a temperature of 11° to 16° C., and were left in the sun at a temperature of well over 50° C. for twelve successive days. At the end of this period they were returned to the water and re-established normal cirral movement within six hours. We ourselves have recorded a temperature of 36·3° C. inside the mantle cavity of *Chthamalus stellatus* at Plymouth, while the barnacles were still attached in their normal position on the rocks, and this was not by any means on the hottest day in the summer.*

On the other hand Cole (1932) says, " . . . Contrasted to the marked resistance when the valves are closed is the extreme sensitivity of the open barnacle to environmental stimuli. Intense stimuli cause immediate withdrawal of the cirri and closure of the valves. Mild stimuli cause irregularity of the cirral movements, . . . Included in such effective stimuli are not only a great variety of chemical compounds, but decrease in illumination (shading reflex), changes in temperature, mechanical vibrations, rate of water flow and contact stimuli."

In Cole (1929) he gives the temperature at which the maximum rate of cirral movement is obtained as 21·0° C. Below 2° the movement was irregular, as it was between 21° and 27°, where also it was often accompanied by closure of the valves, and above 27° they invariably closed.

Runnström (1925) gives the sea surface temperatures at Herdla as 14–15° C. in summer and about 4° C. in winter. He points out that in th first vegetative year there are two periods of shell growth corresponding to the two times of year when the sea is at its mean temperature. In the barnacles at Port Erin there is some indication of this same double growing period of the shell associated with the time of mean temperature, although it is not always traceable. There is also (Moore, 1935, p. 264) decrease in the rate of production of tissues during the period of highest temperature in some barnacles, although this seems to be conditional on the state of sexual maturity of the animal.

An examination of the data given by Johnstone, Scott and Chadwick (1924) for the plankton of Port Erin Bay shows that while there is a considerable variation in the numbers of nauplii and of cypris taken in different years, yet there is no apparent connexion between this variation and the sea temperature. Thus 1912, 1913 and 1917 were years in which very high numbers of nauplii were taken, and the sea temperatures during the February–April period of these years were respectively 4·2% and 5·6% above the mean and 24·0% below it. Further, the years in which there were large numbers of cypris larvæ were not necessarily those in which there had been large numbers of nauplii. In fact it seems likely that the abundance of larvæ near the shore is more dependent on the degree of their dispersal by currents.

Fischer-Piette (1929) gives the limiting values found by him for some of the factors at la Rance. Prennant and Teissier (1929) state that this species is unable to withstand low salinities, but at la Rance it was found in water with a salinity as low as 0·45°/$_{\circ\circ}$. The range of variation of oxygen and pH which they could withstand was considerable. The oxygen concentrations of the waters in which they were found to be living ranged from 26·0 to 5·8 mgm. per litre, and the pH from 9·3 to 7·5. E. Krepps also has published several papers on the relation of the oxygen consumption of barnacles to salinity, temperature, etc.

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* I am indebted to Dr. L. E. Bayliss for assistance in recording these temperatures, which were measured with a small thermocouple inserted into the mantle cavity of the barnacle.

Barnacles are strongly favoured by water bearing a large amount of suspended matter on which they can feed, as in the case of the estuary of the River Tamar, but this may be counterbalanced by pollution of the water resulting in smaller size of the barnacles, as is found in the River Mersey.

The Effect of Crowding.

Barnacle larvæ will frequently settle on all the available rock surface, and so close that when metamorphosed they are touching their neighbours on all sides. Such overcrowding must result in a heavy mortality, since there is not room for a tenth as many adults, but how the selection takes place is not known. In fairly still water it is probable that the presence of a large number of barnacles will seriously deplete the stock of food in the water to their mutual detriment.

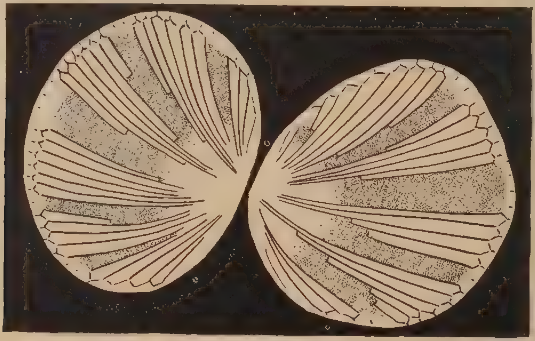

Fig. 6.—Diagram of the basal plates of two specimens of *Balanus improvisus* which settled in contact at one point, but free elsewhere. The tracks of the radial canals show that growth has been unilateral. × 10.

If two barnacles settle so that they are too close together on one side, but are free from obstruction in other directions, they are able to move their bases sideways as they grow, so that, while remaining touching at one point, their centres move apart. The tracks of the radial canals in the basal plates of the *B. improvisus* shown in Figure 6 give evidence of such a shift. If the growing barnacle is crowded on all sides, its only opportunity for growth is upwards, and the result may be a barnacle

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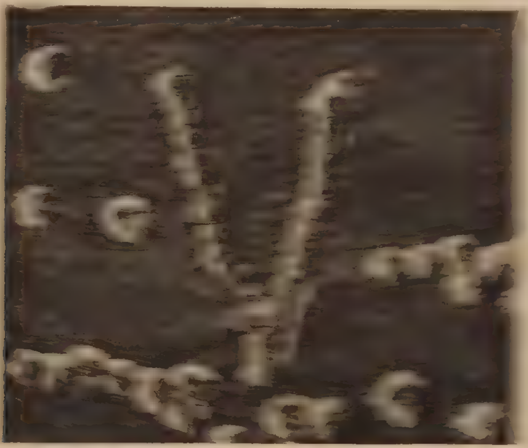

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obtain as much food as the isolated barnacles growing near by. This seems to be a likely factor in retarding the growth of barnacles living in crowded clusters.

In this connexion, there is a form of *B. balanoides* which calls for note, namely var. *elongatus* Gould (Fig. 8). I have received specimens of it from the River Mersey by the courtesy of Prof. J. H. Orton, and have also collected them at Meols in Cheshire. Starting from a narrow base, these barnacles widen towards the apex, until they are frequently ten times as tall as they are wide at the base. It is not certain whether this form is not due in some cases to their having commenced life in a very crowded community, but this is certainly not always the cause since many of them showed no signs of having been attached at the sides to other barnacles. In addition most of those found growing at Meols were isolated. Also many of the latter were colonised round the apex by a younger brood, and sometimes these in turn by a third as may be found in *Balanus hameri* (Moore, 1934, 2). Since there was plenty of uncolonised surface for attachment alongside it would appear that this was in some way undesirable for attachment, and that the barnacle grew so as to carry their orifices as far away from it as possible. Those taken in the Mersey were growing on Liverpool landing stage in a strong current (maximum 5–7 knots), in very muddy and polluted water. The salinity varied from 23 to $28^{\circ}/_{00}$ in summer and from 21 to $27^{\circ}/_{00}$ in winter. The pH is normal.*

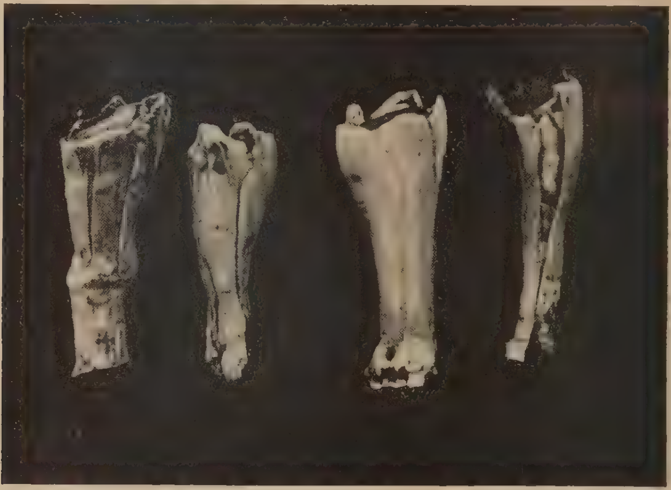

FIG. 8.—*B. balanoides* var. *elongatus* Gould. from the River Mersey. × 1·5.

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* Figures kindly supplied by Mr. J. H. Fraser.

The conditions at Meols were more normal, although the water was far from clear, and the piles on which the barnacles were growing were above a bottom of mud.

SETTLEMENT OF THE LARVÆ.

Vischer (1928) described how the cypris larvæ of Balanus move about the surface on which they settle, apparently testing it, until they find a suitable place to metamorphose. He states (p. 330) that this process may last for over an hour, and that during it the larvæ may travel as far as twelve millimetres. It has also been shown (Vischer, 1928 ; Vischer and Luce, 1928 ; and Neu, 1933) that the settling cypris is negatively heliotropic, and that for lights of equal intensity it is most responsive to green. Finally, if there is a continuous flow of water over the surface of attachment, the barnacle will tend to attach and metamorphose with its long axis along the direction of flow of the current (see p. 296).

On the shore it is frequently seen that the barnacles have settled closely along cracks and grooves in the rocks, like those shown in Figure 7. The barnacles in such grooves are frequently orientated with their long axes along the groove. On the open rock surface, on the other hand, they are apparently orientated haphazard. The much higher degree of concentration of barnacles in the grooves than on the neighbouring smooth surface (see Fig. 7), shows that the cypris must have explored the surface and chosen by preference the shelter of the groove. Possibly they may do this on account of the slightly lower level of illumination there, or possibly for the actual shelter from dislodgement, but this is improbable since Fischer-Piette (1932) has shown that more larvæ settle on exposed rocks than in quiet waters. He also states that the numbers of larvæ settling on the shore are greatest at low water, but that the actual number is not simply related to the number of hours during which that level is covered by the sea. The effect is not therefore due to larvæ settling at a uniform rate for a period of time which is dependent on the period of immersion of the particular level, but is modified by some controlling factor. In the Isle of Man, where a greater number of levels were compared, it was found that the newly settled barnacles were distributed in this way, with the greatest numbers near low water, but that the level of maximum spat settlement was at a varying height above their lower limit, and in some cases as high as half-tide mark.

THE EFFECT OF CURRENT.

The effect of currents in producing large barnacles of the type associated with wave-exposed localities has already been described (p. 284). The reason is perhaps to be found in the fact that in moving water more food will be brought within reach of the animal in a given time than in still water.

A second effect is found in the orientation of barnacles growing in a current of constant direction, but this is rarely found on the open shore where the direction of flow of the water is continually changing under the action of waves. It has been shown (Moore, 1933) that *Balanus improvisus* growing in a continuous current, or in an intermittent current of constant direction, tend to settle with their long axes along the current. Immediately after metamorphosis the barnacle commences to rotate, as is shown by the record kept by the radial canals in the base of the shell. These canals follow the successive positions of the wall plates of the shell, and show that the barnacle has gradually rotated through about 90° (Fig. 9).

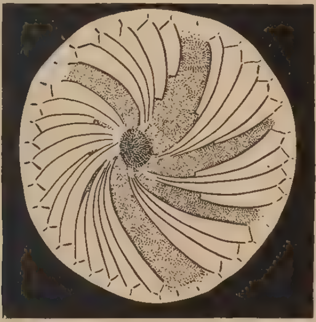

FIG. 9.—Diagram of the basal plate of a specimen of *Balanus improvisus* growing in a current of water. The tracks of the radial canals indicate rotation through about 90°.

After this, in older specimens, rotation has stopped completely and growth has been simply radial.

Since *B. balanoides* has a membranous base it does not retain any such individual record, but the same process may be traced by estimating the mean deviation from the current of successive sizes of barnacles in a suitable locality. Such a situation was found on the inner side of the wooden piles of Fairlie Pier in the Clyde. These were to a large extent sheltered from wave action, and at the same time were subject to a steady tidal current of about two knots. The locality was examined in June, 1934, when the angular deviation from the direction of the current was measured for 198 young barnacles of 1–4 mm. long and of the 1934 brood, and for 204 individuals, 16–23 mm. long and several years old. The results are shown in Figure 10, and indicate clearly the change from the alignment of most of the spat along the current to the adult condition with most of the barnacles lying across the current. Actually the observed results could have been produced by a selective action in which those few barnacles which had settled across the current survived more readily than those which had settled along it, but in view of the positive evidence from *B. improvisus* it seems more likely that they rotated.

Observation of a barnacle when feeding suggests a possible reason for this rotation. The cirri together form a cup-shaped net, and in normal feeding movements in still or very slightly moving water this net is alternately extended and retracted along the same plane in which it normally lies in the shell. Occasionally, however, if the temperature is not too low, this movement may be varied, and the cirri may be held extended for a second or more and sometimes twisted to one side. If a current of water is passed over the barnacle, certain results tend to be produced, although not invariably seen. If the barnacle is lying so that the current impinges on the back of its net of cirri, it frequently retracts its cirri and closes its shell, obviously finding difficulty in capturing any food particles in its net. If, however, the barnacle is facing in the opposite directions, so that the water impinges into its cirral net the barnacle tends to stay extended for a longer period, especially if the current is strong,

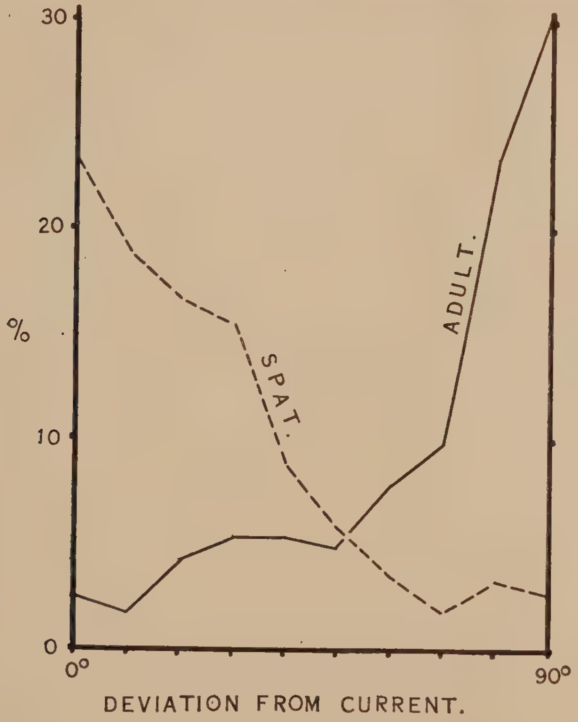

Fig. 10.—Distribution diagram of *B. balanoides* on Fairlie Pier, in terms of angular deviation from the direction of flow of the current: young and adults.

and retraction then becomes dependent on some particle touching the cirri. Clearly this method of feeding, while equally effective, will require less expenditure of energy on the part of the barnacle.

If the barnacle is lying at right angles to the direction of the impinging current, it frequently extends its cirri, and then turns them at right angles so that the whole net faces up the current, in which position it holds them until contact with a food particle stimulates contraction. Clearly then, the best position for a barnacle to take up when feeding in a current of water is that in which its cirral net is facing up the current, and when not naturally facing in this direction it can twist its body through as much as 90° so as to face in the required direction. Apparently, however, it is unable to twist through more than about a right angle. Where, therefore, a barnacle is situated in a strong tidal current which reverses its direction of flow periodically, orientation along the current would allow the barnacle to feed for only half the period during which the current was sufficiently strong to effect it, whereas feeding could be continuous if the shell were orientated across the current and the body always twisted in the required direction. And since the cypris larva normally settles with its long axis along the current, a twist through one right angle will achieve the desired result. In the case of the *B. improvisus* mentioned above, some of the barnacles were growing in a stream of water which was always in the same direction, and never reversed. The bases of the barnacles showed, however, that they had rotated through 90° only and then stopped. After metamorphosis of a cypris larva in a current of water, the newly-formed barnacle would be orientated with its cirri facing down the current of water in a position most disadvantageous for capturing food, and rotation would clearly be desirable. Perhaps when the shell has been rotated far enough for the cirri to be twisted into the direction of the current, the stimulus to rotate the shell ceases.

Relation to Other Dominant Organisms.

In the Irish Sea and the North Sea the dominant intertidal barnacle is *B. balanoides*. Along the western end of the English Channel coast its place is largely taken by *Chthamalus stellatus*, and Fischer-Piette (1928 and 1934) has given an account of their distribution in this region. At the western end, Roscoff on the French side and the Scilly Isles on the English side, Chthamalus is common at all levels, and *B. balanoides* either absent or restricted to the lowest levels. Progressively eastwards Balanus becomes more common and extends upwards to higher levels, while Chthamalus becomes rarer and finally disappears. In sheltered localities, where Chthamalus thrives less well than Balanus, the process of replacement takes place further west than it does on exposed headlands. At the western limit of their distribution the Balanus are small and do not produce any larvæ.

At Port Erin, Chthamalus does not normally occur, although it was recorded as abundant in one locality there in 1886 (Marrat, 1886). As it has not been recorded since it seems likely that this was an abnormal year in which larvæ were carried by current to the Manx shores which they infected, but where they did not survive as an established species. The species is present in small numbers in the Clyde Sea Area, and Dr. J. A. Kitching has found it recently at Loch Sween.

At all the localities examined in the Isle of Man, the lower limit of distribution of *B. balanoides* was fairly sharply defined, and below this their place was taken by the polychæte worm, *Spirorbis borealis* Daudin. As the latter occurs abundantly in small areas uncolonised by Balanus although above the barnacle's lower limit, it would appear that Balanus is dominant and that Spirorbis grows only where the barnacle is not able to.

The presence of large algæ such as *Fucus* spp., *Ascophyllum nodosum*, etc., is definitely harmful to the barnacles, and in most places they are not found within touching distance of them ; in the River Tamar at Plymouth, however, where the water is extremely rich in suspended food material, *B. balanoides* has been found thriving and very large under a heavy carpet of Ascophyllum. This suggests that the harmful effect of the algæ is at least in part due to their screening the barnacles from an adequate food supply.

The chief enemy of barnacles is *Nucella* (=*Purpura*) *lapillus*, whose main food they are. This species is found feeding on barnacles practically everywhere, but it does not penetrate so far into brackish water as does *B. balanoides* (Fischer-Piette, 1931), and in very wave beaten situations the Nucella are unable to feed on the open rock surfaces in rough weather, and are in consequence fewer in numbers. Day (1880, p. 204) quotes a statement of McIntosh's that barnacles are eaten by *Blennius pholis* at St. Andrew's. Elmhirst (1922) also states that in the upper levels the newly settled barnacles are eaten by *Littorina saxatilis* (=*L. rudis*). I have not been able to obtain confirmation of this, nor to observe that the Littorina do more than shelter in the already empty shells of dead barnacles, and browse on the algæ infecting the shells of the older ones.

Finally Allison and Cole have recently demonstrated the interesting fact that *B. balanoides* is sensitive to the constitution of the plankton in the water in which it is feeding, remaining closed when peridinians are abundant, but opening and feeding when the plankton is comprised of diatoms and other organisms.

Estimate of the Total Barnacle Population of the Shore and its Annual Food Output.

The figures given in the tables at the end of this paper allow a calculation to be made of the total amount of barnacles on a metre-wide strip of shore running vertically from high to low water at each locality. So far as numbers of individuals are concerned, if we omit the first year spat, the amount rises steadily with increasing wave-exposure, but if the spat are included the numbers are greatest at Port Erin (Fig. 11). This is accounted for by the smaller average size at Port Erin and hence the possibility of a greater number per unit area of crowded population. When, however, weights are compared, and these are the most adequate measures of the amount of barnacle present, the values rise steadily with increasing exposure, the values being, in order of increasing exposure, 7, 27, 106 and 542 gm. of dried tissue.

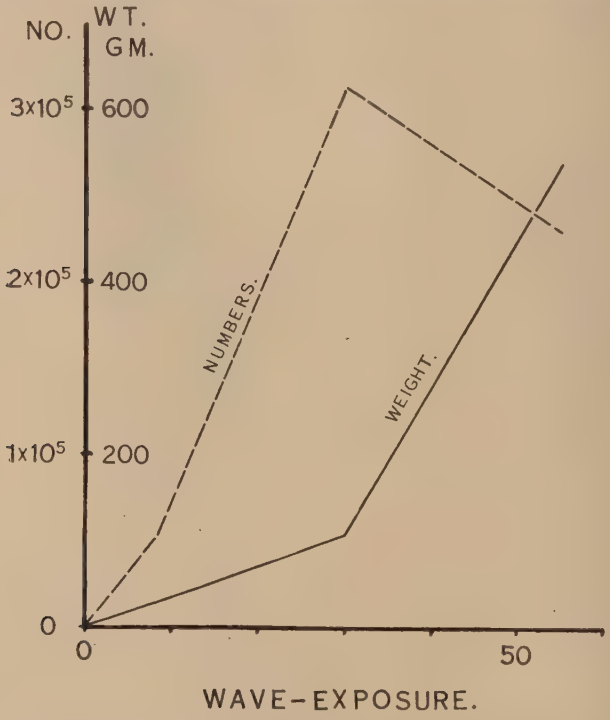

Fig. 11.—The relation between amount of barnacles (numbers and weight of tissue) on a metre-wide vertical strip of shore, and wave-exposure.

These figures apply only to a vertical plane surface of rock, but it is of interest to obtain some estimate of the total amount of barnacles on the shore. If we multiply such figures by two for the increased area of a sloping shore, and multiply again by two for the increased area due to irregularities of the surface (a minimum figure in the latter case), we have a very rough approximation of the amounts on normal stretches of shore of the types studied. This gives a value of about two thousand kilogrammes of dried tissue per kilometre of normal shore of the degree of wave-exposure found outside Bradda, and about eight hundred kilogrammes for the Port Erin type of shore.

Not all this amount of total available food is liberated into the sea each year, but a figure for the output may be obtained. Runnström states that at Herdla most barnacles die after their first spawning when they are a little over two years old, a possible few only surviving to spawn a second time. At Port Erin the observed mortality of a small number of over four months old was 35% at B.1, and 21% at B.2 (Moore, 1933). And at +4′ 10″ outside Bradda in July, one-year-old barnacles (excluding that year's spat) formed about half of the population. If we apply Runnström's figures we get the following results. On a metre-wide vertical strip outside Bradda, the 86,000 barnacles in their second or subsequent year would mostly die. Their dry weight is 516 gm., so that they would contribute about 400 gm. dry weight of tissue to the sea. The addition to this of first-year spat would be relatively small. At Port Erin the first-year spat would yield about 40 gm., and the older barnacles about a further 40 gm., or 80 gm. in all. These figures would be equivalent to a yearly output of about 1600 kgm. of tissue per kilometre of normal shore of the Bradda type, and 320 kilogramme for the Port Erin type.

If, however, we take a mortality rate based on the mean of the values for B.1 and B.2, namely 28 per cent per annum, we get an output of 600 kgm. per kilometre outside Bradda, and 200 kgm. at Port Erin. The former is more affected by the change since its population contains a much larger proportion of older individuals.

In addition to this contribution to the sea in the form of body, most of which passes through the stage of Purpura meat, there is an output of organic matter as excreta, as moulted exoskeleton and as larvæ. Of the first two we know nothing, but we are able to estimate the amount of the larval output. To consider first the Bradda type, we must divide the shore into the part above mid-tide level where the barnacles do not spawn until their second year, and the area below this level where they spawn in their first year. Above mid-tide a vertical metre-wide strip will contain 56,000 barnacles of which about half are mature spawners. The average size of the 28,000 spawners is 90·6 mm^3., and their larval output at this size will be 4200 larvæ each, or a total of 117 million larvæ. Below mid-tide level there are 31,000 spawners with an average size of 58·1 mm^3., and average output of 2500 larvæ, and a total output of 77 million. The output from all levels together would therefore be about two hundred million larvæ per year, or about a million million larvæ per year per normal kilometre of shore.

For the Port Erin type of shore the output may be similarly estimated at about twenty million larvæ from a metre-wide vertical strip, or about a hundred million per normal kilometre of shore.

Taking the weight of a single nauplius as $7{\cdot}5 \times 10^{-4}$ mgm. (Moore, 1935), we get an output of about 600 kgm. dry weight of larvæ per kilometre of the Bradda type of shore per year in addition to the 600–1600 kgm. of body tissues. At Port Erin there would be 90 kgm. of larvæ in addition to the 200–320 kgm. of body. In a very wave-exposed locality, therefore, the contribution to the sea in the form of larvæ is equal in importance to the contribution in the form of general body tissues, whereas in a more sheltered type of locality the larvæ form a relatively small part of the year's output.

In conclusion I wish to express my indebtedness to the staffs of the Plymouth and Port Erin laboratories, and to Mr. R. Elmhirst at Millport, for assistance and advice in this work, and also to Dr. E. Fischer–Piette, Dr. J. A. Kitching and Prof. J. H. Orton.

SUMMARY.

1. Vertical traverses down the shore were worked at four localities in the Isle of Man, with varying degrees of wave-exposure, for which factor a coefficient is given.

2. The upper limit of distribution is high water neaps in a sheltered place, and up to high water of extreme spring tides at greater wave-exposure. The lower limit similarly drops with increasing exposure.

3. Barnacles are largest and most abundant in a wave-exposed locality. The effect of wave-exposure may be reproduced by a current.

4. In sheltered localities the optimum level for growth, mean size, etc., is at low water for newly settled barnacles, but moves progressively up to high water as they grow older. In a very exposed situation, however, the optimum is always at low water.

5. In an exposed situation the gonads mature in their first year below about half-tide level, and in their second year above this level. With decreased wave-exposure the age of maturation rises, especially at high water until in a very sheltered place few barnacles mature at all.

6. Limiting values for temperature, salinity, oxygen concentration, pH, etc., are given, so far as they are known.

7. Barnacles which are crowded together grow very much more slowly than do isolated individuals.

8. Barnacles grow more rapidly in a current of water. They also tend to orientate themselves with the current—along it when newly settled, and then, by rotation, across it as adults. This is apparently to facilitate feeding.

9. The interrelation with other littoral species is described.

10. The total barnacle population of the shore is calculated. Outside Bradda it amounted to about a thousand million individuals per normal kilometre of shore with a yearly output of about six hundred kgm. of tissue (dry weight), and their yearly output of about a million million larvæ weighing a further 90 kgm.

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TABLE I.

Distribution of *B. balanoides* Outside Bradda Head, 8th July, 1933. Exposure Factor 55.

First year.

Level.	Average volume. mm^3.	Average weight. mgm.	Amount per sq. metre. Number.	Amount per sq. metre. Weight. gm.
+ 9′ 8″	–	–	0	0
+ 7′ 6″	0·29	–	1,600	*ca.* 0·06
+ 7′ 2″	0·45	–	16,000	*ca.* 0·51
+ 6′ 5″	0·75	0·046	32,000	1·47
+ 0′ 0″	2·31	0·118	40,800††	4·82
– 5′ 5″	8·51	0·544	32,000	17·40
– 5′ 11″	–	–	0	0

Second year and older.

Level.	Average volume. mm^3.	Average weight. mgm.	Amount per sq. metre. Number.	Amount per sq. metre. Weight. gm.
+ 9′ 8″	–	–	0	0
+ 7′ 6″	89·2	6·98	100	0·7
+ 7′ 2″	50·3*	3·31‖	15,900**	52·7
+ 6′ 5″	76·8†	6·54	20,000	131
+ 0′ 0″	49·6‡	5·38	32,000	173
– 5′ 5″	111§	12·1	4,700	56·8
– 5′ 11″	–	–	0	0

* 14·2 mm^3. 2nd year ; 83·4 mm^3. 3rd year and older.
† 24·5 mm^3. 2nd year ; 83·2 mm^3. 3rd year and older.
‡ 36·9 mm^3. 2nd year ; 92·7 mm^3. 3rd year and older.
§ 73·5 mm^3. 2nd year ; 209 mm^3. 3rd year and older.
‖ 0·861 mgm. 2nd year ; 5·56 mgm. 3rd year and older.
** 7600 2nd year ; 8300 3rd year and older.
†† Up to 200,000 per sq. metre if available clear space.

TABLE II.

DISTRIBUTION OF *Balanus balanoides* ON THE DUB REEF, PORT ERIN. 28TH JUNE, 1933. EXPOSURE FACTOR 30.

Level.	Average volume. mm^3.	Average weight. mgm.	Amount per sq. metre. Number.	Weight. gm.
		First year.		
+ 9′ 0″	–	–	0	–
+ 5′ 4″	*ca.* 1·03	*ca.* 0·097	*ca.* 200	*ca.* 0·02
+ 4′ 10″	1·03	0·096	8,800	0·85
+ 2′ 4″	2·48	0·226	84,800	19·2
+ 0′ 10″	1·60	0·144	70,000	10·1
– 0′ 8″	1·85	0·163	60,800	9·92
– 1′ 6″	1·92	0·167	110,000	18·4
– 4′ 0″	2·83	0·237	118,000	28·0
– 6′ 2″	3·00	0·246	29,300	7·21
– 7′ 2″	3·00	0·240	3,000	0·72
– 7′ 8″	–	–	0	–
		Second year and older.		
+ 9′ 0″	–	–	0	–
+ 5′ 4″	*ca.* 61·8	*ca.* 5·82	*ca.* 30	*ca.* 0·17
+ 4′ 10″	61·8	5·88	1,800*	10·6
+ 2′ 4″	28·0	2·85	8,500	24·2
+ 0′ 10″	5·3	0·56	19,300	10·9
– 0′ 8″	6·7	0·74	13,000	9·48
– 1′ 6″	13·3	1·49	26,000	38·8
– 4′ 0″	11·0	1·32	7,900	10·4
– 6′ 2″	–	–	0	–

* 1340 2nd year ; 460 3rd year and older.

TABLE III.

DISTRIBUTION OF *B. balanoides* ON THE ALFRED PIER, PORT ST. MARY. 3RD JULY, 1933. EXPOSURE FACTOR 8.

Level.	Average volume. mm^3.	Average weight. mgm.	Amount per sq. metre. Number.	Weight. gm.
		First year.		
+ 5′ 6″	–	–	0	–
+ 5′ 4″	0·33	–	2,500	*ca.* 0·04
+ 4′ 3″	0·35	–	20,400	*ca.* 0·04
+ 3′ 3″	0·34	–	14,000	*ca.* 0·23
+ 2′ 0″	1·00	–	15,300	*ca.* 2·21
– 1′ 4″	1·06	–	900	*ca.* 0·17
– 1′ 9″	–	–	0	–
		Second year and older.		
+ 5′ 6″	–	–	0	–
+ 5′ 4″	55·6	2·70	3,400‡	9·18
+ 4′ 3″	20·5*	1·27†	14,600§	18·6
+ 3′ 3″	14·4	0·71	33,600	23·9
+ 2′ 0″	5·83	0·73	18,500	13·5
– 1′ 4″	2·59	0·47	2,400	1·13
– 1′ 9″	–	–	0	–

* 6·55 mm^3. 2nd year ; 29·4 mm^3. 3rd year and older.
† 0·44 mgm. 2nd year ; 1·80 mgm. 3rd year and older.
‡ 600 2nd year ; 2,800 3rd year and older.
§ 5,700 2nd year ; 8,900 3rd year and older.

TABLE IV.

DISTRIBUTION OF *B. balanoides* ON THE INNER PIER, PORT ST. MARY. 12TH JULY, 1933. EXPOSURE FACTOR 0.

Level.	Average volume. mm³.	Average weight. mgm.	Amount per sq. metre. Number.	Amount per sq. metre. Weight. gm.
		First year.		
+ 3′ 8″	–	–	0	–
+ 2′ 6″	0·48	–	5,300	*ca.* 0·08
+ 1′ 8″	0·61	0·02	10,300	0·21
– 0′ 4″	0·81	0·07	10,400	0·73
– 0′ 10″	–	–	0	–
		Second year and older.		
+ 3′ 8″	–	–	0	–
+ 2′ 6″	2·67	0·18	500	0·09
+ 1′ 8″	3·78	0·32	3,500	1 12
– 0′ 4″	3·63	0·35	400	0·14
– 0′ 10″	–	–	0	–

TABLE V.

AMOUNTS OF BARNACLES ON A VERTICAL STRIP OF SHORE ONE METRE WIDE. JUNE–JULY, 1933. NUMBERS AND DRY WEIGHTS OF TISSUE.

Locality.		Outside Bradda Head.	Dub Reef, Port Erin.	Alfred Pr., P. St. Mary.	Inner Pr., P. St. Mary.
Exposure factor		55	30	8	0
First Year	Number	142,000	265,000	23,000	11,400
	Weight gm.	26·2	53·2	1·87	0·38
Second year and older	Number	86,300	45,600	31,000	1,800
	Weight gm.	516	52·9	26·0	6·65
Total: all ages	Number	228,000	311,000	54,000	13,200
	Weight gm.	542	106	27·9	7·03

On the Value of Certain Plankton Animals as Indicators of Water Movements in the English Channel and North Sea.

By

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With 6 Figures in the Text.

THE use of plankton animals as "indicators" of water movements has been constantly considered in the past, notably by Cleve, Aurivillius, Gran and Kramp. The distribution of oceanic and neritic species in the English Channel has been fully discussed by Gough (1905, b) and Bygrave (1911). There is a gradual increase in the percentage of oceanic species from east to west. Bygrave distinguished between permanent and periodic oceanic forms, the occurrence of the latter being "probably greatly influenced by purely Hydrographic causes, such as the Ocean Currents and the inflow of Atlantic water into the Channel." He placed in the latter group "such species as *Chætoceras peruvianum*, *Rhizosolenia hebetata*, *Muggiæa atlantica*, *Euchæta hebes*, and *Limacina retroversa*." There is, however, doubt about the identity of the Limacina. Gough (1905, a) showed that Muggiæa enters the English Channel from the south-west. Gough (1905, b) has also shown how *Euchæta hebes* and Farran (1911) how *Oithona atlantica* may enter the Channel at times.

But the different plankton associations that can be regarded as indicative of water conditions in the mouth of the Channel have not yet been clearly defined. If plankton animals are to be used as indicators they should be *practical* indicators, and therefore the larger and more easily identifiable they are the better. I hope to show in this report that we have a number of good indicators among the larger plankton animals, whose occurrence or absence off Plymouth is a reflection of water conditions far removed from this area itself.

Since 1930 the weekly ring-trawl collections have been studied with this end in view. A complete list of the numbers of different species taken in the 2-metre stramin ring-trawl off Plymouth in 1930 and the beginning of 1931 was published to act as a basis for comparison for the succeeding years (Russell, 1933, a). In that paper the following species were regarded as characteristic of the year in question, *Aglantha rosea*, *Liriope exigua*, *Stephanomia bijuga*, *Clione limacina*, and *Meganyctiphanes norvegica*.

In 1928 Meek drew attention to the fact that in the North Sea the two species of Sagitta, *S. elegans* and *S. setosa*, showed marked differences in their numerical proportions from year to year, and were probably indicative of different water masses. Accordingly, since 1930 special attention has been paid to the life-histories of these two species in the Plymouth region and their occurrence from year to year. A paper has already been published giving the fluctuations in the Sagitta populations in the years 1930, 1931, and part of 1932 (Russell, 1933, b). Notes have also been published on the occurrence of certain pelagic tunicates and on the siphonophore Muggiæa (Russell and Hastings, 1933 ; Russell, 1934). In the present paper these results have been brought together and carried on into the first months of 1935.

THE SAGITTA POPULATIONS AND ASSOCIATED FAUNA OF "WESTERN" AND "CHANNEL" WATERS.

The numbers of *S. elegans* and *S. setosa* caught in the half-hour oblique hauls with the 2-metre stramin ring-trawl at a position two miles east of the Eddystone Lighthouse during the period October, 1932, to February, 1935, are shown in Figure 2. I have also reproduced in Figure 1 the diagram that was published in the previous report (Russell, 1933, b) showing the sequence of events from February, 1930, to September, 1932. In these figures the curves for the numbers of the two species are shown in the top halves of the diagrams (*S. elegans*, unbroken line ; *S. setosa*, broken line). In the lower halves of these diagrams are given the percentage proportions of the two species in each catch (*S. elegans*, black ; *S. setosa*, white). In the previous report it was shown that while *S. elegans* completely predominated in the catches from February to September in 1930, in October, 1930, *S. setosa* started to appear and became dominant in September, 1931. After this there were two slight increases of *S. elegans* in January and in August in 1932 (see Figure 1). Figure 2 shows that the dominance of *S. setosa* has continued up to the present time, February, 1935, with the exception of two short increases of *S. elegans* from March to June in 1933 and in May, 1934, and a further indication at the present date. On no occasion, however, was *S. elegans* seen in anything approaching the very large numbers caught in the earlier period of these observations in 1930 and 1931.

It had at first been thought that these two species might normally always be present together in this area, and that the predominance of one species over the other might be the effect of success or failure in the reproduction of one or other species. That this was probably not so was first indicated by a study of the life-histories of the medusæ occurring off Plymouth. In attempting to link up certain of the medusæ with their hydroids special attention was given to the species *Cosmetira pilosella*, which is sometimes very abundant here during the summer months and the hydroid of which has not yet been identified. In this study, which was started in 1932, the complete absence of the earliest stages of this medusa was striking. Although examining plankton samples caught with silk tow-nets almost daily I never found a very early stage that could be attached to this species. In fact only one such probable individual has ever been recorded from Plymouth (Browne, 1896, p. 486). The distribution of Cosmetira is given by Kramp as British Coasts from Channel to Shetland Islands; North Sea and Kattegat; West Coast of Norway to Bergen (Kramp, 1933, p. 570). In an earlier paper Kramp (1919, p. 63) goes rather fully into the distribution of this species and says "Browne has found quite young specimens at Valencia Harbour both in May and August" (see Browne, 1900, p. 719). The absence of young specimens of Cosmetira in the Plymouth waters at once suggests that its hydroid does not live in this region and that the medusæ we catch here have beencarried in the water masses from some other region in which the hydroid has its normal habitat. Browne's record of young specimens from Valencia indicates the possibility that the hydroid is to be found in the deeper water along the Atlantic shores of the British Isles.

Now observation of the occurrence of Cosmetira in the Plymouth ring-trawl catches during the summer months showed that this species was only to be found when *S. elegans* was also present. If *S. elegans* was present in numbers throughout the summer the period of occurrence of Cosmetira was very prolonged, for instance in 1930 it was present from April until September (see Table 1, in Russell, 1933, a). In 1934 *S. elegans* only occurred in numbers in May, in that year Cosmetira also appeared in May and then disappeared for the remainder of the summer as did *S. elegans*. A similar agreement between the occurrence of these two species was also shown for the other years (see Figure 4 on page 318). The significance of the decrease in Cosmetira in June and July, 1931, is not obvious: it was shown by other plankton animals and also occurs to a lesser extent in 1933.

This then is a definite indication that when *S. elegans* becomes numerous off Plymouth it is being brought here from elsewhere. Owing to the occurrence of young Cosmetira at Valencia it was natural to seek for *S. elegans* in the waters south of Ireland. Fortunately that area is worked at intervals each year by the Irish Fishery Department and I was able to enlist the co-operation of Mr. G. P. Farran who very kindly supplied me with samples of Sagitta collected in that area in the years 1921, 1930, and 1934; in 1930 and 1934 *S. elegans* and *S. setosa* predominated respectively off Plymouth, while in 1921 both species were common at the Sevenstones. The area covered by the Irish investigations lies between latitudes

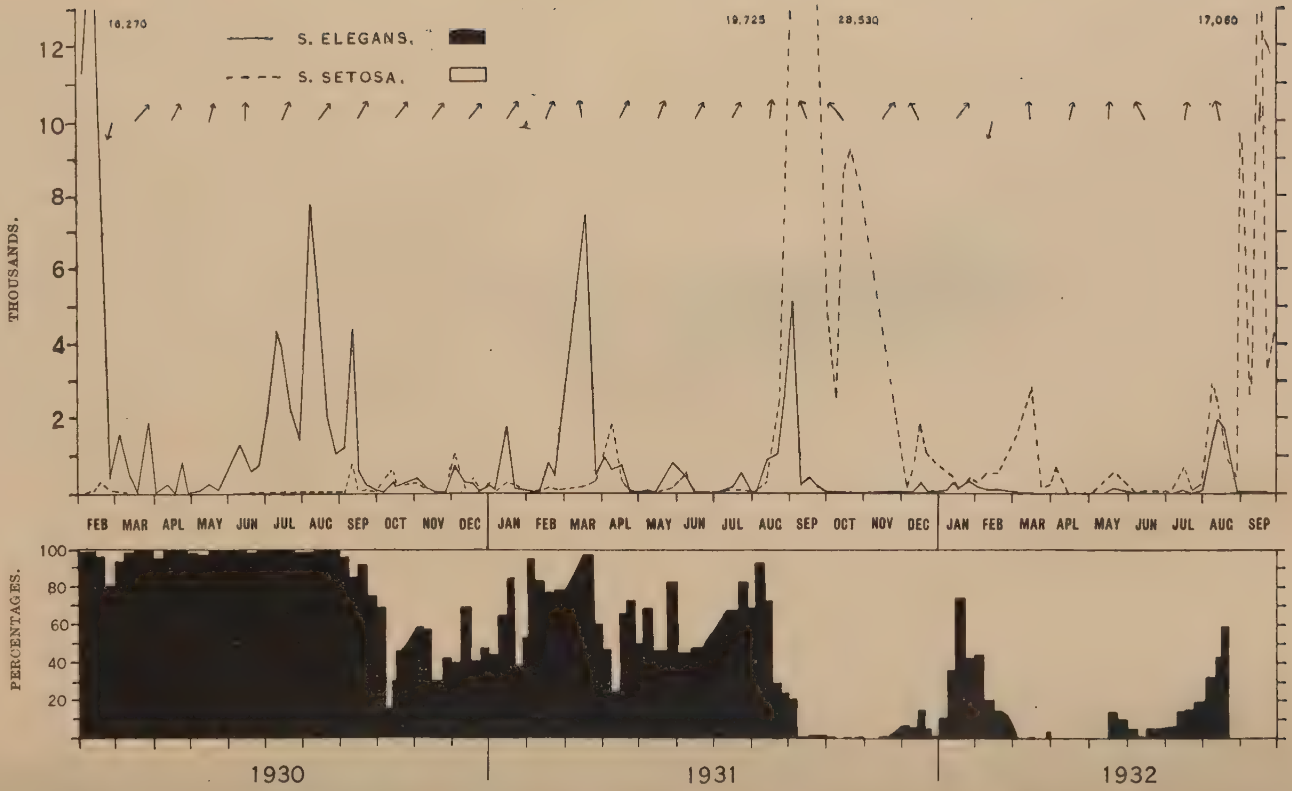

FIG. 1.—Above, curves showing the actual abundance of *S. elegans* (————) and *S. setosa* (– – – – –) in half-hour oblique hauls with the 2-metre ring-trawl made usually at weekly intervals during the period February, 1930, to September, 1932. (The numbers are in thousands.) Below, the percentage composition of the Sagitta populations during the same period; *S. elegans*, black; *S. setosa*, white. At the top of the diagram the arrows indicate the mean direction (true) of flow of water through the Straits of Dover for each month as indicated by the Carruthers Current Meter working from the Varne Lightship.

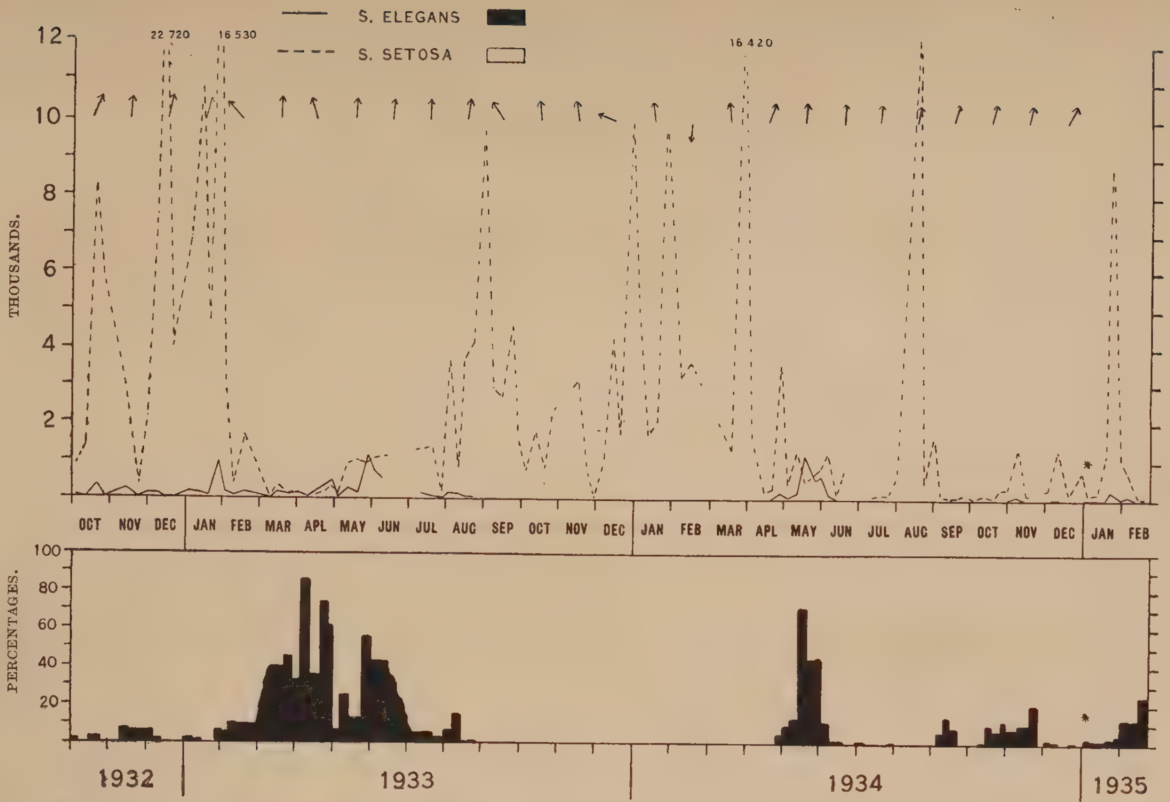

FIG. 2.—Above, curves showing the actual abundance of *S. elegans* (————) and *S. setosa* (– – – – –) in half-hour oblique hauls with the 2-metre ring-trawl made usually at weekly intervals during the period October, 1932 to February, 1935. "*" denotes that the collection was made at night. (The numbers are in thousands.) Below, the percentage composition of the Sagitta populations during the same period; *S. elegans*, black; *S. setosa*, white.

At the top of the diagram the arrows indicate the mean direction (true) of flow of water through the Straits of Dover for each month as indicated by the Carruthers Current Meter working from the Varne Lightship.

50°54′N. to 49°20′N. and longitudes 6°21′W. to 11°17′W. (see Figure 3). Examination of the Sagitta material collected in that area at different times of the year showed that in the years 1921, 1930, and 1934 *S. elegans* alone was present and no *S. setosa* were seen.* It is evident therefore that *S. elegans* lives in a body of water quite distinct from that in which *S. setosa* lives.

This was further confirmed by the examination of plankton samples taken from the Sevenstones Lightship in the years 1913 to 1928. In these samples *S. elegans* was always present and only at certain times did *S. setosa* appear in any numbers, notably in 1921. Clearly the boundary between the populations of these two species of Sagitta lies somewhere about Land's End. Following this up an attempt was made in January, 1934, to define more exactly the regions occupied by the two species. Unfortunately this cruise in S.S. *Salpa* was cut short by weather conditions, and it was only possible to make collections on a line between Plymouth and the Lizard. Even so, the results were quite definite and showed a gradual change over from a population off Plymouth in which *S. setosa* predominated to one in which *S. elegans* was becoming the most abundant species. The actual proportions of the two species were as follows.

		S. elegans.	*S. setosa.*
Jan. 21, 1935.	2 m. East of Eddystone	2·3%	97·7%
,, 24, 1935.	14 m. W.S.W. of Rame Head† . . .	4·3%	95·7%
,, 24, 1935.	22 m. ,, ,, ,, . . .	28·3%	71·7%
,, 24, 1935.	33 m. ,, ,, ,, . . .	49·3%	50·7%
,, 24, 1935.	Off Lizard	53·6%‡	46·4%
,, 29, 1935.	2 m. East of Eddystone	4·1%	95·9%

Having established that the two species of Sagitta occupy different water masses it remained to examine the results of the ring-trawl collections off Plymouth over the period of years 1930 to 1935 to see whether the occurrence of other plankton animals could be linked with either one or other species of Sagitta.

Examination showed that the following species occurred only when *S. elegans* was present in numbers in the catches,‖ *Aglantha rosea*, *Stephanomia bijuga*, *Cosmetira pilosella* (in spring and summer only), *Clione limacina*, *Meganyctiphanes norvegica*, *Thysanoessa inermis*, and three specimens of *Sagitta serratodentata*.

Only in 1930 did all these species occur together and it can be assumed that the large quantities of *S. elegans* present in that year, to the exclusion of *S. setosa*, indicated that a considerable body of water had moved into the Channel from the south of Ireland carrying its planktonic fauna with it. In future in this report the water which carries these indicators will be alluded to as " western " water. In the other years when *S. elegans* only appeared spasmodically in small numbers it may be regarded as indicating that there were only minor influxes of " western " water, since the next most abundant species, Aglantha, Cosmetira, and Stephanomia, alone appeared in small numbers with *S. elegans*.

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* Two badly preserved specimens in 1921 were identified as ? *S. setosa*, but it is doubtful if they were.

† Haul taken in the dark.

‡ Aglantha also present.

‖ All names of species in this report are those used in the Plymouth Marine Fauna, 1931.

All the above species are boreal or arctic boreal species whose occurrence off the south of Ireland is well known and has been shown by the plankton investigations of the International Council. The breeding and distribution of Meganyctiphanes has been worked out in detail for that area by Frost (1932) and the species is shown to occur all over the region investigated. Its presence on the Smalls and Cockburn Bank has also been indicated by Hickling (1925). *Sagitta serratodentata* is a pure oceanic species, and its occurrence may be taken as an indication that the " western " water flowing past Plymouth in 1930 was drawn from well out towards the Atlantic.

In the International plankton investigations Meganyctiphanes was recorded for the English Channel as a species " which has never been taken, except at one station in the Western part in November 1907 " (Kramp, 1913, p. 540). It is significant that exactly the same is said of *Clione limacina* and that this species also was only recorded from the Channel in 1907 (Paulsen, 1911, p. 53).

In 1924 Lebour (1924) recorded both Meganyctiphanes and Thysanoessa off Plymouth. We have no records of Sagitta throughout that year, but in June at any rate *S. elegans* predominated.

The positions of the stations from which the catches of Sagitta were examined from the south of Ireland in 1921, 1930, and 1934, are shown in Figure 3. In this figure the area that has been shown to be populated by *S. elegans* is indicated by diagonal shading. We do not know how much further this area extends to the south. It may perhaps stretch right across the mouth of the Channel, or it may be reasonably expected that the area changes and lies in fact in the region of cylonic circulation known to exist at the mouth of the Channel south of Ireland (see p. 321). A small area well to the south, in the Bay of Biscay, was studied by Fowler's " Research " Expedition. This area has been indicated in Figure 3. Aglantha, Meganyctiphanes and *Sagitta serratodentata* were caught in that area. Browne (1906) recorded that 42% of the medusæ were *Aglantha rosea* and 27% *Aglaura hemistoma*. It might be supposed that if the " western " water came from as far south as the " Research " area Aglaura would have been noticed here with Aglantha. But it has never been seen in the Channel. It is in fact a warm water species, and probably its northern limit of distribution slightly overlaps the southern boundary for Aglantha. A further indication that " western " water does not come from so far south is that no *Clione limacina* were found in the " Research " collections (Pelseneer, 1906). Paulsen (1910, p. 52) also says of Clione, " Here, south of Ireland, I found *Clione* repeatedly from the ' Thor ' in 1906, but only north and east of the steep slope towards the deep Atlantic. In the Bay of Biscay proper I have not found a single specimen, although in search of *Clione*. Thus it is likely that we have the southern limit of its distribution here." This

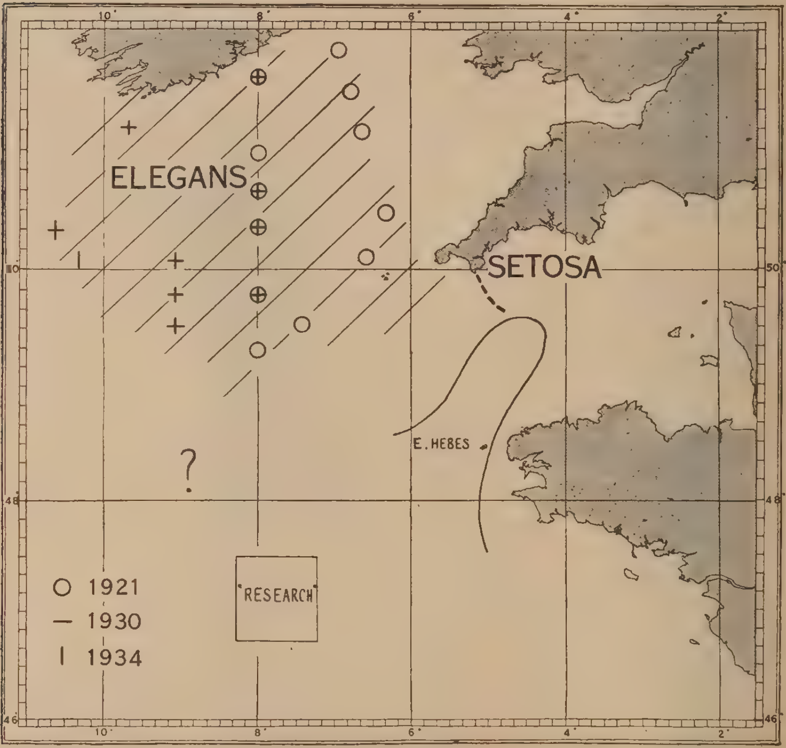

Fig. 3.—Chart showing the positions of the stations south of Ireland from which collections were examined for 1921, 1930 and 1934. Only *S. elegans* were found and the shaded area indicates " western " water. The position of the boundary between " western " water as indicated by *S. elegans* and " Channel " water as indicated by *S. setosa* is shown for 1934.

The small rectangle indicates the region in which the " Research " Expedition worked.

The distribution of *Euchæta hebes* is indicated after Farran (1911, Plate XIV). This is the limit within which the species occurred on at least 20% of the occasions on which observations were made.

species was caught further south on the " Michael Sars " North Atlantic Expedition but only in the deeper layers in the open Atlantic (see Bonnevie, 1933, p. 60). However, " during the Southern crossing it was found to belong to a water-layer with a temperature as low as from 4° to 10° C."

It has been shown above that there are a certain number of plankton animals that can be regarded as indicators of " western" water. So far, however, in the ring-trawl catches it has not been possible to find any species that can be linked alone to *S. setosa.* The distribution of this species is gone into fully below (see p. 322) and it is concluded that it is a purely neritic species. If this be so it is at present the sole indicator we know of what I shall henceforth call " Channel " water.* It is, however, not possible to fix the other indicators, if they exist, without a similar close survey of the plankton population of the " western " water to see which species, commonly present in " Channel " water in association with *S. setosa*, are at the same time absent in " western " water.

In another paper in this Journal (Russell, 1935, p. 170) I have drawn attention to the agreement shown between the abundance of the young of summer spawning fish and the phosphate content of the water in the previous winter. The occurrence of low phosphate values coincides with the periods in which *S. setosa* predominates and it seems likely that this low phosphate content is a characteristic of " Channel " water. The abundance of plankton animals as shown by the ring-trawl catches in the summer months is certainly much less when " Channel " water predominates off Plymouth than when " western " water predominates.

THE PLANKTON FAUNA OF " SOUTH-WESTERN " WATER.

From time to time certain plankton animals appear off Plymouth whose normal habitat is undoubtedly in warmer waters. Among the most obvious of these are the pelagic tunicates, Salps, and Doliolids, the siphonophores, Muggiæa, and the medusa, *Liriope exigua.* Gough (1905) has shown how in 1904 *Muggiœa atlantica* penetrated the Channel from the south-west and gradually extended its distribution over the neighbouring waters. As a result of the International plankton investigations the occurrence of a warm water copepod, *Euchæta hebes*, was shown by Gough (1905, b). Farran (1911) has indicated graphically how the distribution of this species may extend into the mouth of the Channel as a tongue stretching from the south-west past Ushant (see Figure 3).

Farran points out " the connection between the distribution of this species and the presence of a tongue of highly saline water running across

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* Künne (Wulff, Bückmann and Künne, 1934) says of Channel water that the lack of indicators is especially characteristic.

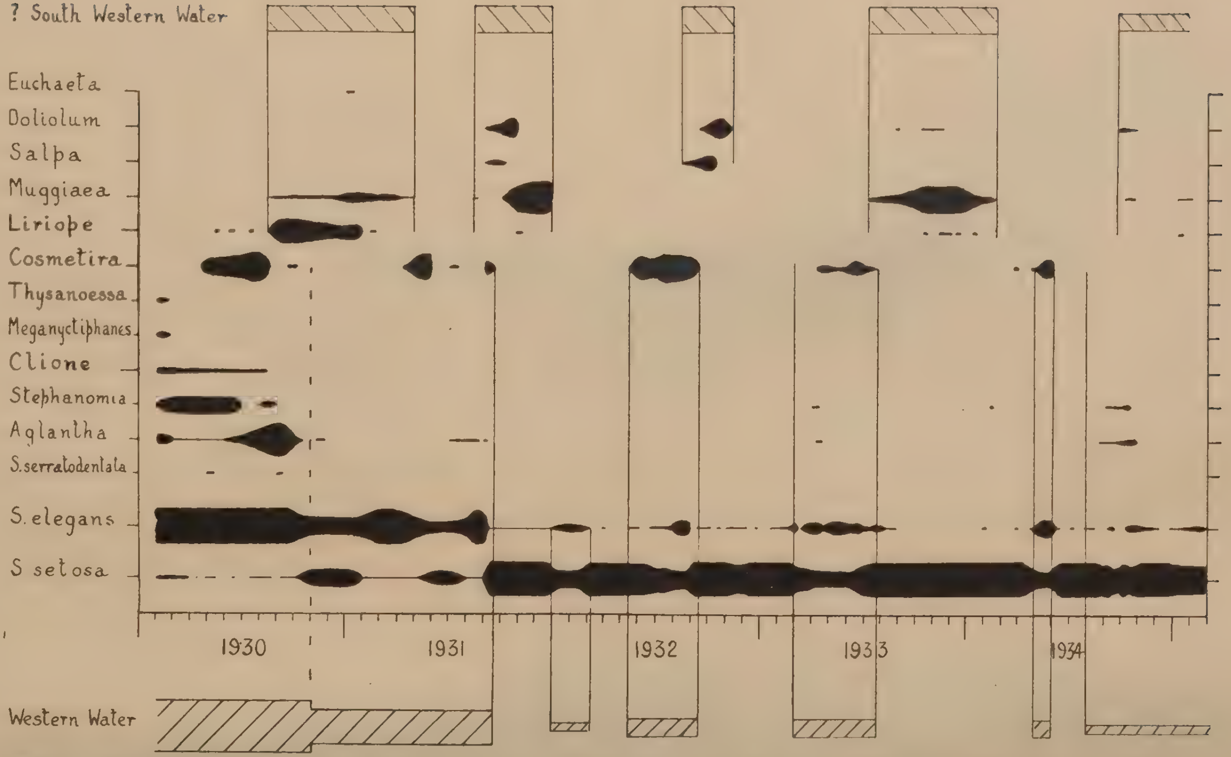

FIG. 4.—Diagram showing the occurrence of the various planktonic indicators in collections off Plymouth during the period February, 1930, to February, 1935.

The species shown are *Sagitta setosa*, *S. elegans*, *S. serratodentata*, *Aglantha rosea*, *Stephanomia bijuga*, *Clione limacina*, *Meganyctiphanes norvegica*, *Thysanoessa inermis*, *Cosmetira pilosella*, *Liriope exigua*, *Muggiæa kochi*, *Salpa democratica* (1931), *Salpa fusiformis* (1932), *Doliolum nationalis* (1931 and 1932), *Doliolum gegenbauri* (1931), and *Euchæta hebes*.

the mouth of the Channel." He remarks that the most frequent occurrence of this species coincides with the area of mean salinity of 33·4%. He also comments on the fact that this species had never been met with in the course of the Irish Investigations on the south and west coasts of Ireland, that is in "western" water.

The occurrence of the pelagic tunicates and of Muggiæa off Plymouth in recent years has already been noted (Russell and Hastings, 1933; Russell, 1934). The occurrence of these animals and of Liriope in the ring-trawl catches off Plymouth since 1930 is shown graphically in Figure 4. It can be seen that these species show no association with *S. elegans* and they are here regarded as possible indicators of "south-western" water. That this may be true is strengthened by the record of the occurrence of *Euchæta hebes* in 1931 when Muggiæa was abundant. At that time the complete contents of the ring-trawl catches were examined; in the later years only the easily observed "indicators" alluded to have been picked out. If Euchæta occurred at other times in association with the "south-western" fauna it will have been overlooked. It is surely significant also that in the International plankton investigations from 1902 to 1908 the only year in which this species was not seen was 1907, that is the only year in which Clione and Meganyctiphanes were recorded in the Channel (see above, p. 315, and Farran, 1911, p. 94). In addition Farran (1911, p. 104) records that the deeper living and more northerly copepod, *Oithona atlantica*, which is distinctly oceanic, spread up the Channel to an unusual distance in 1907.

In regarding the pelagic tunicates and Muggiæa as indicators of "south-western" water caution is needed. These are species which can reproduce asexually, and it is possible that at times their numbers will thus be increased so rapidly as to give the false impression that there has been a movement of a large body of water. This might especially be so if the water were unusually warm. In this connexion, therefore, Liriope may possibly be regarded as the better indicator. In Figure 4 it is noticeable that the "south-western" water indicators seem usually to follow the disappearance of the "western" water. It appears almost as though this might indicate that we have here a seasonal phenomenon rather than an indication of water movement, the warm water species increasing when the water is sufficiently warmed. But if this were so the disappearance of *S. elegans* is hard to explain; and the absence of *E. hebes* in 1907 indicates that in that year water may not have come from the south-west, but from the west as shown by the presence of Clione Meganyctiphanes, and *Oithona atlantica* (see also p. 315). It should perhaps also be mentioned that whereas such animals as Cosmetira, *S. elegans* (except July to September), and the Euphausiids live in the daytime in the deeper water layers (Russell, 1927), Salps, Doliolids, and Muggiæa are not so bound to the depths and strong southerly winds might carry them along in the surface layers in sufficient numbers to seed the area. The occurrence of floating organisms such as Velella and Ianthina in 1932 (Russell and Kemp, 1932) was an indication of this.

The full sequence of events showing the occurrence of the indicators representative of the three bodies of water—" western," " Channel," and " south-western "—since 1930 is shown diagramatically in Figure 4.

The Relation between the Plankton " Indicators " and the Hydrographic Conditions.

Since the conclusions arrived at in this report have been based on observations in only a single locality it is not possible to draw any close comparison between the presence of the plankton indicators and the hydrographic data collected over the whole of the western half and mouth of the English Channel. Furthermore, it is doubtful if the hydrographic observations are sufficiently closely spaced in time and space to indicate for certain the direction from which water is entering the Channel. In an area where several water bodies mix, also, the plankton animals alone can give the clue as to the water's origin unless the salinity differences are marked.

Such outlines of the hydrographic conditions as can be obtained from the data have been given by Harvey (1930 and 1934). A comparison with these and later unpublished data shows at most that there is no considerable discrepancy between such deductions as can be drawn from the sequence of events shown in Figure 4 and the hydrographic data. Especially is it noticeable that *S. elegans* is generally to be found off Plymouth when water of high salinity has entered the Channel, and that *S. setosa* predominates during periods of low salinities.

It has been shown by Harvey (1934, p. 739) that the distribution of salinity in the western half and mouth of the Channel reflected the nature of the movements of water through the Straits of Dover as shown by Carruthers' (1928) current measurements from the Varne Lightship. It seemed, therefore, of interest to compare the fluctuations in the Sagitta population off Plymouth with the conditions of passage of water through the Straits of Dover. I am greatly indebted to Dr. J. N. Carruthers for supplying me with data on the flow of water past the Varne Lightship for the whole period of my observations. He has kindly allowed me to publish the data given in Figures 1 and 2.* In a recent publication Carruthers†

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* Since the above was written these data have appeared in print (Carruthers, 1935). Table II in this new report by Carruthers presents the data used in this present paper. His Appendix 6 gives the substance of his British Association paper quoted under Carruthers (1934).

† See also Ministry of Agriculture and Fisheries Report on Sea Fisheries for the year 1933 (1934, pp. 47–49).

(1934) says, " The results of the last three years are of especial interest, for, instead of the residual current heading boldly into the North Sea (as it most frequently has done in the previous three years) it has displayed less and less easting with the passage of time. During 1933 the current headed about half a point west of north."

I have inserted at the tops of Figures 1 and 2 the idealized directions (true) of the daily flow for each month of the residual current through the Straits of Dover. The decrease in the easting alluded to above is very obvious and it is significant that the change has taken place at the time when *S. elegans* gave way to *S. setosa* in 1931. On the whole there is agreement also in that the periods when *S. elegans* is most abundant off Plymouth tend to coincide with the periods of strongest flow through from the Channel to the North Sea. Under these circumstances apparently " western " water flows past Plymouth.

It is not expected that agreement can be shown at this stage in every detail between plankton indicators and hydrographic data, but at any rate sufficient relation has been indicated to prove that a study of these organisms, in conjunction with the hydrographic observations, over the whole area might prove a valuable aid to the elucidation of the water movements. Indeed the following on of the occurrence of " south-western " water after the disappearance of " western " water alluded to on page 319 is quite in accord with previous ideas on the water circulation off the mouth of the Channel (see Matthews, 1914, and Lumby, 1925). The " western " water probably arises from the cyclonic circulation to the south of Ireland. This cyclonic circulation " whose southern limit in winter is approximately in the latitude of the Scilly Islands, extends as far south as Ushant in summer " (Lumby, 1925, p. 12). The mouth of the Channel thus becomes partially blocked and water can only enter from the south-west bringing with it the " south-western " fauna. There is thus an indication from the plankton observations of a pulse of " western " water entering the Channel with its maximum about May. This pulse retreats as the pulse of Atlantic water entering the North Sea from the north increases; and this is followed by a pulse of " south-western " water into the Channel.

It has already been remarked (p. 317) that there is an indication that the " western " water is richer in phosphate than the Channel water. It is therefore interesting to read the following quotation from Matthews (1914, p. 22): " This circulation may prove to be of considerable biological importance. The water off the south-east coast of Ireland, and in the southern edge of the cyclonic circulation off the fairway to the English Channel, has travelled a long distance since it last left the open ocean, and if, as seems probable, there is any difference, other than temperature and salinity, between oceanic and shore waters, then this water might be poorer in the minute constituents of oceanic water and richer in those of coastal water than would be expected on the ground of its distance from the open sea." Actually the indications are that relatively the coastal water is poorer in nutrient salts, and it seems likely that the enrichment of the " western " water is due to upwelling along the Atlantic slope (see also Thomsen, 1933, for the North Sea).

The Geographical Distribution of *Sagitta setosa.*

Sagitta setosa appears to be a plankton animal with a rather limited distribution. It has only been recorded from the English Channel, the North Sea, Skagerak and Kattegat. Meek (1928, p. 756), in commenting on the occurrence of this species off the Northumberland coast in such years as 1921, when the flow of Atlantic water into the North Sea from the north was strong, has suggested that the species may be brought there from the Atlantic. This species together with *S. elegans* has been consistently confused with the warm-water species *S. bipunctata* and it is possible that future investigations may show that its area of distribution actually stretches further than that given above. There are, however, a few points worthy of mention that indicate that this may not be the case.

We owe the first full descriptions for distinguishing between the above three species of Sagitta to Ritter-Záhony. These descriptions were published by him in his report on the Chætognatha of the Plankton Expedition (1911). In this report Ritter-Záhony deals with collections made in the Atlantic both off the mouth of the English Channel and round the north of Scotland. Yet he makes a point of mentioning (1911, p. 11) that *S. setosa* had then only been found in the North Sea, Skagerak, and Kattegat, and English Channel. If the species had occurred in collections from the open Atlantic he at any rate is not likely to have overlooked them.

Almost all the holoplanktonic animals occurring in the northern waters on the eastern side of the Atlantic have been shown to live also on the American side. Yet *S. setosa* has never been recorded from the western Atlantic and if it occurs there it is not likely to have been overlooked by Huntsman who has studied the variations of *S. elegans* in such detail (1919).

In 1933 I had the opportunity of cruising in more northern waters in Col. E. T. Peel's yacht, *St. George*. A sample of plankton taken off the Yorkshire coast on August 2nd, 1933, (54°31′N. : 0°0½′W.) yielded large numbers of *S. setosa* with only one or two *S. elegans*. But in samples that I took in the Shetland Isles, in Balta Sound (13.vii.33) and in Luning Sound (14.vii.33), there were no *S. setosa*, but only *S. elegans* together with

Aglantha. Similarly only *S. elegans* and Aglantha appeared in a collection made in Loch Eriboll (25.vii.33) on the north coast of Scotland, while these two species with large numbers of Cosmetira were present in collections made north of the Fair Isle Channel (9.vii.33; 59°42′N.; 2°10′W.). There was therefore no evidence that *S. setosa* was living in the Atlantic waters in the north.

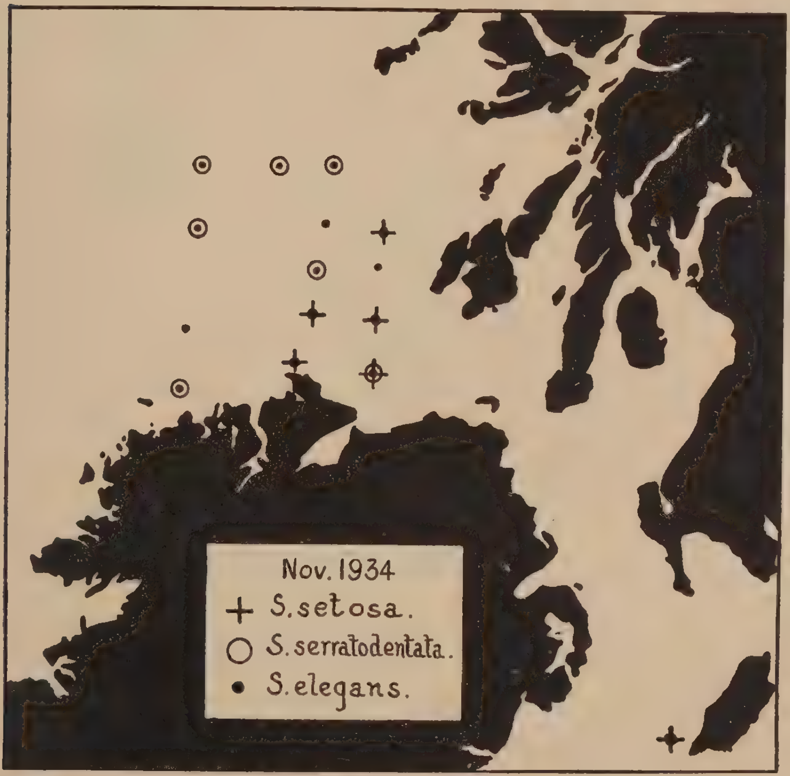

FIG. 5.—Chart indicating the positions of occurrence of the three species of Sagitta off the north coast of Ireland and at Port Erin in November, 1934.

I am indebted to Mr. W. C. Smith, the curator of the Port Erin Laboratory, for allowing me to see samples of plankton taken off the Isle of Man in the Irish Sea in 1934. In November a number of *S. setosa* were found although *S. elegans* had predominated earlier in the year. Samples of Sagitta caught off the North Coast of Ireland in the same year, 1934, have also been kindly sent me by Mr. G. P. Farran. *S. setosa* only occurred there in November, and then only in small numbers at the stations nearest to the entrance to the North Channel into the Irish Sea (see

Figure 5). It is likely that these had filtered out from the Irish Sea where they were numerous at that time of year. These *S. setosa* in the Irish Sea may have been a local race, or may have drifted up from the English Channel round Land's End and through the St. George's Channel. Examination of a number of samples taken in different localities in the Irish Sea in the years 1909, 1913, and 1925, showed an almost entire preponderance of *S. elegans*.

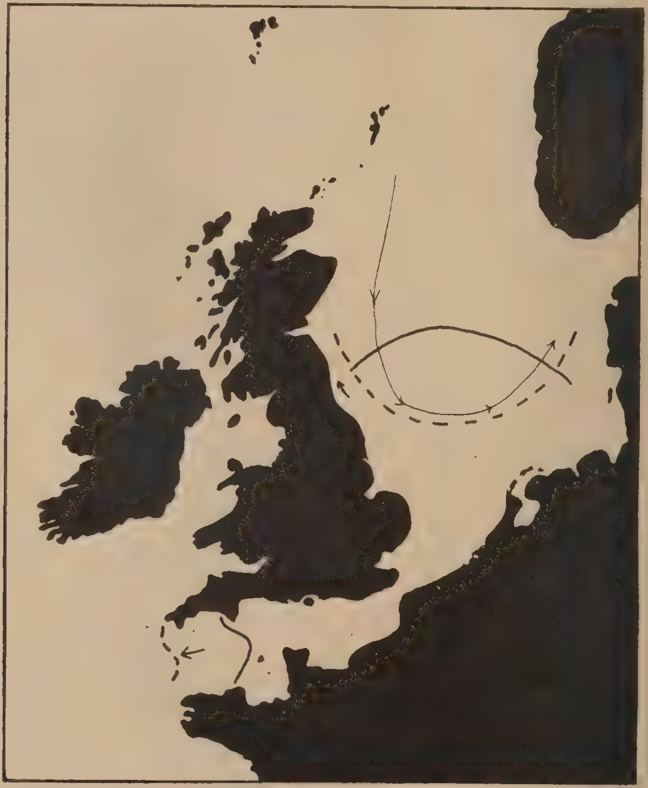

Fig. 6.—Chart showing the hypothetical centre of distribution of *Sagitta setosa* in the North Sea and English Channel (unbroken line boundaries) and the change in distribution effected by an increase of flow of Atlantic water from the north into the North Sea (broken line boundaries).

In the area sampled north of Ireland *S. elegans* was found at all stations, while at the outermost stations to the west and north the more oceanic *S. serratodentata* was common (Figure 5).

The above evidence seems to indicate very strongly that *S. setosa* is a purely neritic species, with its main centre of distribution in the southern North Sea and English Channel. As such it may be expected to have rather a similar distribution to that of the neritic copepod *Centropages hamatus*. If this be so the fluctuations in the numbers of *S. elegans* and *S. setosa* off Plymouth would appear to give a striking confirmation to the theory put forward by Carruthers (1934) that "the Dover Straits current waxes and wanes through the year in a sort of buffer relationship with the current from the north—that there exists a sort of see-saw conflict between the two." In Figure 6 I have drawn a hypothetical distribution for *S. setosa*, based on that of *C. hamatus* (Scott, 1911, Plate XVIII), showing how an increased flow of Atlantic water from the north into the North Sea would tend to push the *S. setosa* population, or "Channel" water towards the mouth of the Channel, while an increased flow from the Channel through the Straits of Dover into the North Sea would tend to bring the "western" water with *S. elegans* past Plymouth. At the same time an increased flow of water into the northern North Sea would bank up the southern North Sea water and some might tend to flow up the east coast of England thus carrying *S. setosa* further north than usual. This would account for the predominance of *S. setosa* on the Northumberland coast in 1921 as shown by Meek ; it is significant also that in 1921 *S. setosa* was unusually abundant at the Sevenstones.

It is evident that we are greatly in debt to Professor Meek for drawing attention to the value that these two Sagitta species may have as indicators of the origins of water masses.

In conclusion it should be pointed out that at this stage it is unsafe to attempt to draw definite deductions. At most we have a somewhat hazy picture ; yet the indications are clear enough to show that the problem is worth following up in greater detail. It is especially desirable that the limits of the distribution of the different species concerned should be more closely defined over the whole area.

THE POSSIBLE VALUE OF SAGITTA AS AN INDICATOR OF CONDITIONS IN AREAS FAR REMOVED FROM PLYMOUTH.

Since all the species in association with *S. elegans* are boreal or arctic boreal species it is likely that they will also prove of value as indicators of Atlantic water entering the northern North Sea, as indeed is already indicated by Künne* (in Wulff, Bückmann and Künne, 1934, p. 334).

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* I did not see the data given by Künne (1934) until after this report was finished. Künne gives as indicators for the south-west Dogger Bank swirl *Cosmetira megalotis*, *Aglantha digitalis*, *Nyctiphanes couchi*, *Agalma elegans*, *Clione limacina*, *Limacina retroversa*, the larvæ of *Luidia sarsi*, and *Oikopleura labradoriensis*. Of these *C. megalotis* is very closely allied to *C. pilosella* ; and *A. rosea* recorded in this paper is regarded by some as a variety of *A. digitalis*. It is interesting also that Künne should regard the larvæ of Luidia as indicators, since off Plymouth in the late summer of 1930 Luidia larvæ were very abundant ; both *L. sarsi* and *L. ciliaris* young were recorded (see Plymouth Marine Fauna, 1931, pp. 291–292). Although *N. couchi* occurred in large numbers in 1930 with *M. norvegica* it is doubtful whether it can be regarded as a reliable indicator of "western" water as it is the least oceanic of the Euphausians occurring here. At any rate its presence should only be regarded as significant if it is unusually numerous.

Mention has been made in the Annual Reports of the Fishery Board for Scotland for the years 1930 to 1933 of certain organisms that have characterised the waters rounding the North of Scotland from year to year. Stephanomia was recorded (as Agalmopsis) in 1930; in that year it was especially abundant off Plymouth. Amongst other species of medusæ Cosmetira and Laodicea are mentioned for 1931; although no reasons have been found as yet for regarding Laodicea as an indicator in the Channel region it is interesting that in the summer of 1931 Laodicea was very much more abundant off Plymouth than in any of the other years under review. In 1932 *Cyclosalpa bakeri* was recorded from the North of Scotland; in that year salps occurred off Plymouth although a different species, *Salps fusiformis.*

In 1931 *Doliolum gegenbauri* was recorded for the first time off Plymouth; in 1933 this species appeared in the North Sea (Lucas, 1933).

Savage and Hardy (1935) have for a number of years been studying the occurrence and distribution of large concentrations of the diatom *Rhizosolenia styliformis* in the southern North Sea. This diatom has been regarded as an indicator of Atlantic water. If the presence or absence of large patches of Rhizosolenia in the southern North Sea be compared with the variations in the Sagitta population off Plymouth a certain amount of agreement is shown. For instance, in the years 1930 and 1931 when *S. elegans* was predominating at Plymouth there were no concentrations of Rhizosolenia in the area studied in the North Sea. In 1932, when *S. setosa* predominated off Plymouth, Rhizosolenia was abundant in the North Sea. Although for previous years full data are not available for Plymouth, what evidence we have strongly supports the above indication. In 1921, when *S. setosa* was very abundant at the Sevenstones, Rhizosolenia occurred in the North Sea. In 1924, when Meganyctiphanes occurred off Plymouth and in which year *S. elegans* was at any rate predominating in July, an absence of phytoplankton was recorded in the North Sea. This is further evidence that the two populations of Sagitta swing to and fro off Plymouth according to the strength of the flow of Atlantic water into the North Sea from the north. When this flow is strong Rhizosolenia is carried in the Atlantic water, rich in phosphates (Thomsen, 1933), to seed the region of the south-west Dogger Bank swirl, and in the Channel *S. elegans* becomes pushed away to the westward so that *S. setosa* is brought into the neighbourhood of Plymouth.

Examination of the Sagitta results for 1933 and 1934 shows that with the predominance of *S. setosa* off Plymouth Rhizosolenia is likely to have occurred in the southern North Sea in both years. Furthermore seeing that *S. elegans* was entirely absent off Plymouth in the autumn of 1933, but present in small numbers in 1934, it seemed likely that a greater volume of Atlantic water passed into the North Sea from the north in

1933 than in 1934. Thus it would be expected that the conditions were suitable for producing a bigger flowering of Rhizosolenia in 1933 than in 1934. Actually the Rhizosolenia concentration was very dense in 1933 (see Min. Agric. Fish. Report on Sea Fisheries for the year 1933 (1934, p. 46)), and Mr. R. E. Savage has confirmed by letter that Rhizosolenia occurred in smaller quantities in 1934. If this agreement should be confirmed in the future we shall be in the position of being able to predict from the composition of the Sagitta population off Plymouth what are the chances that there will be concentrations of Rhizosolenia in the southern North Sea in the autumn. Savage and Hardy have further shown that the movements of the Herring shoals are apparently influenced by the occurrence and distribution of these phytoplankton concentrations, and the landings of Herring at Lowestoft and Yarmouth are affected in consequence.

The possible value of Sagitta as an indicator of Herring movements off Plymouth should also be borne in mind. It can now be realised that the Herring spawning in the neighbourhood of Plymouth and along the south Cornish coast visit a region in which either "Channel" water or "western" water may predominate. It is probable that at the spawning period a fish is most susceptible to the physical and chemical conditions of the water. Close watch should therefore be kept to see whether the shoals visiting Plymouth when *S. setosa* predominates are of the same composition and origin as those spawning here when *S. elegans* predominates.

SUMMARY.

The possibility that certain plankton organisms retained by a stramin net may prove of value as indicators in elucidating the water movements at the mouth of the English Channel is shown.

The water populated by *Sagitta setosa* is shown to be clearly demarked from that in which *S. elegans* lives, the latter living to the west of the Channel mouth south of Ireland. The water in which *S. elegans* lives has here been called "western" water.

It is shown that the planktonic indicators for "western" water are *Sagitta elegans*, *Sagitta serratodentata*, *Aglantha rosea*, *Stephanomia bijuga*, *Clione limacina*, *Meganyctiphanes norvegica*, *Thysanoessa inermis*, and *Cosmetira pilosella* (in spring and summer only). *Sagitta setosa* is regarded as an indicator of "Channel" water. Muggiæa, Salps, Doliolids, *Liriope exigua* and *Euchæta hebes* are regarded as indicators of "south-western" water.

The geographical distribution of *S. setosa* is discussed. It is shown that

it is probably a neritic species mainly confined to the English Channel and North Sea.

S. setosa predominates off Plymouth when the easterly element in the Dover Straits current is suppressed and the flow of Atlantic water into the North Sea from the north is strong (Carruthers' Theory). The two Sagitta populations swing to and fro off Plymouth so that, with a strong flow of Atlantic water into the North Sea from the north, the *S. elegans* population is pushed westward to the mouth of the Channel and *S. setosa* occurs off Plymouth.

During the course of the five years, 1930 to 1934, an agreement has been found between the occurrence or absence of concentrations of the diatom *Rhizosolenia styliformis* in the southern North Sea and the variations in the composition of the Sagitta population off Plymouth In the years in which Rhizosolenia, an indicator of Atlantic water, was abundant in the southern North Sea *S. setosa* predominated off Plymouth; when Rhizosolenia was absent *S. elegans* predominated.

These diatom concentrations have been shown by Savage and Hardy to have an apparent influence on the movements of the Herring which is reflected in the landings at Yarmouth and Lowestoft.

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APPENDIX.

Since the above report was written a number of samples of Sagitta have been kindly sent to me by Dr. J. Le Gall, Director of the Marine Laboratory at Boulogne, from catches made during fishery cruises off the mouth of the Channel. Although these samples are too few to show the water movements they confirm the general idea outlined above. Collections were made sometimes further south than the area covered by the Irish investigations and these indicated that the distribution of *S. elegans* might stretch right across the mouth of the Channel. The occurrence of the different species of Sagitta in May and June, 1929, is shown in Figure 7. This clearly indicates that *S. setosa* was confined to the coastal and Channel water and may be carried northwards round Land's End in small numbers.

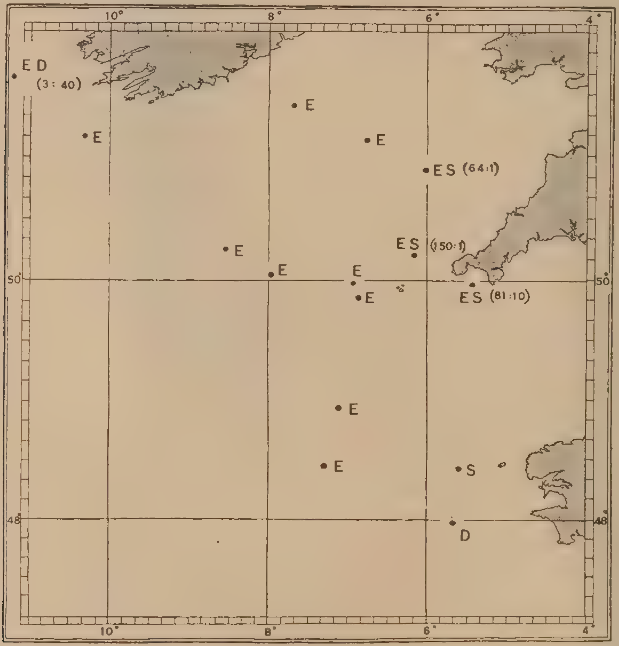

FIG. 7.—Distribution of three species of Sagitta shown by collections made in May and June, 1929. E, *S. elegans* ; S. *S. setosa* ; D, *S. serratodentata*. The figures in brackets show the proportions in which two species occurred together.

These collections enable the following new localities for *S. setosa* to be recorded :

13.vii.25 . .	47° 46′ N. : 4° 13′ W.
1.vi.27 . .	49° 52′ N. : 6° 16′ W.
16.v.29 . .	48° 27′ N. : 5° 33′ W.
29.iv.31 . .	48° 15′ N. : 4° 36′ W.

The Function of the Tegumental Glands in the Statocyst of *Homarus vulgaris.*

By
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With 4 Figures in the Text.

1. Introduction.

Prentiss (1901), in the course of his study of the otocyst (or statocyst as it will be referred to here) of the Decapod Crustacea, found that the statoliths consist of sand grains which are renewed after each moult. These may lie free in the cavity of the statocyst or be attached to the sensory setæ. In the crayfish, *Cambarus affinis*, and in the megalopa stage of the crab, *Carcinus mœnas*, Prentiss found that the sand grains were secured to the setæ by a substance which he considered (though without any direct evidence) to be secreted by the tegumental glands present beneath the integument of the sac. In *Palæmonetes vulgaris*, though he was unable to find similar glands, he found fine ducts which penetrated the integument and these he regarded as the outlets for the glands he could not identify. Herrick (1911) found tegumental glands in the sub-epithelial tissues beneath the integument of the statocyst in *Homarus americanus* and he accepted Prentiss' view as to their function ; Kinzig (1914) came to a similar conclusion after the study of a large number of Decapods.

It has recently been shown by Yonge (1932) that the tegumental glands in *Homarus vulgaris* and in other Decapod Crustacea secrete the cuticle which everywhere covers the underlying and much thicker chitin which is formed by the chitinogenous epithelium. The cuticle is totally different in nature from the chitin and the two can be distinguished by a variety of chemical and physical tests. Yonge also pointed out that the primary function of the glands was not necessarily incompatible with accessory functions such as the binding of the eggs to the pleopods of the female.*

The discovery of the primary function of the tegumental glands enables the re-investigation of Prentiss' theory to be profitably undertaken. The glands situated around the statocyst may be responsible only for the formation of the cuticle which lines the integument of the sac, on the other hand if the substance which binds the statoliths to the sensory setæ in *Homarus vulgaris* (the experimental material used in this research) can be shown to have the same properties as the cuticle, it is not unreasonable to assume that it is formed by the same agency.

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* This has since been confirmed and forms the subject of a forthcoming paper. C.M.Y.

2. Structure of the Statocyst.

The statocyst in *Homarus vulgaris* is situated, as in all Decapod Crustacea, in the basal segment of the first antenna. It consists of an ectodermal invagination on the dorsal side which opens by a small aperture at the anterior end (Fig. 1, AP). Within the cavity are two clusters of sensory setæ (ST). One of these (V) extends over a horseshoe shaped area on the ventral wall, the setæ (Fig. 1, C) being arranged in two rows with an additional third, irregular row on the convex side of the curve. The other (Fig. 1, B) consists of a group of some five setæ situated on a small papilla on the dorsal wall (D) in about the middle line. These setæ are longer than those of the ventral wall.

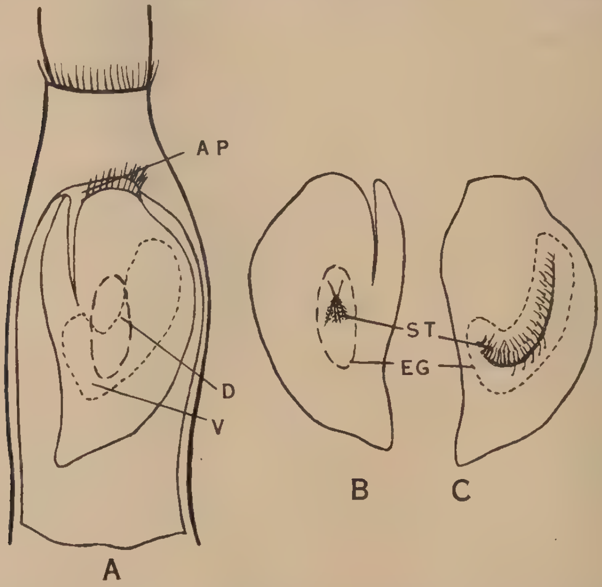

Fig. 1.—Semi-diagrammatic representation of statocyst of *Homarus vulgaris*. ×4. A, dorsal view of basal segment of first antenna of right side showing extent of statocyst; B, roof of cavity; C, floor of cavity; AP, aperture; D, dorsal area of setæ and attached sand grains; EG, extent of sand grains indicated by broken lines; ST, sensory setæ; V, ventral area of setæ and attached sand grains.

The setæ (Fig. 3), which have been described in detail by Prentiss, Kinzig, and earlier workers, are hollow, plumose structures with a spherical membrane (M) at the base which permits of a wide range of movement. The setæ in *H. vulgaris* are not bent at an angle of 120° as described by Prentiss for Palæmonetes. The sand grains (S) forming the statoliths are attached to the setæ, the pinnules of which interlock to form a " wickerlike mesh " (Prentiss), by masses of a hyaline secretion (H). When the statocyst is opened up the sand grains so embedded appear as a wide, irregular semicircle on the floor of the cavity and as an oval mass on the roof. Owing to the extent of the hyaline secretion the area occupied by the sand grains (Fig. 1, EG) is considerably greater than that occupied by the setæ (Fig. 1, ST). The majority of these sand grains become detached from the setæ when they are removed, but examination shows that they are bound together by strands of the hyaline secretion.

3. The Tegumental Glands.

The tegumental glands which occur in the sub-epithelial tissues around the statocyst have the usual structure (see Yonge, 1932, and earlier workers quoted by him). In the anterior region they are especially numerous beneath the dorso-lateral wall (i.e. between the dorsal cluster of setæ and the lateral arm of the ventral horse-shoe area which extends further to the anterior than does the median arm). In the middle region, where both arms of the horse-shoe are cut through in section, as well as

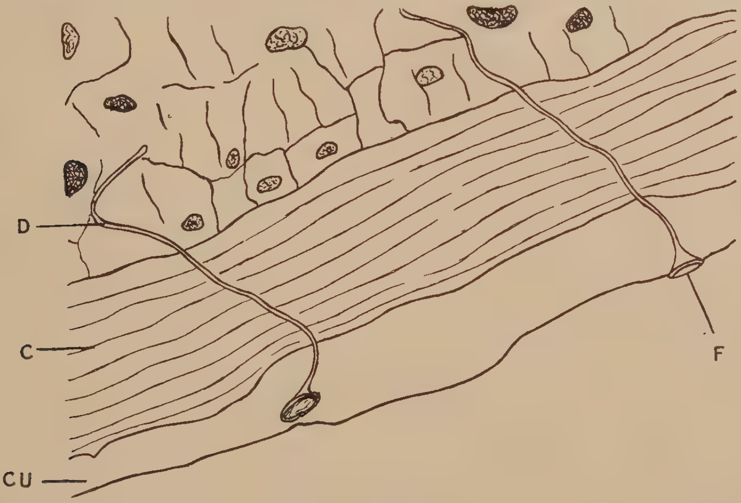

Fig. 2.—Section through wall of statocyst showing passage of ducts from tegumental glands through integument. ×500. C, chitin; CU, cuticle; D, duct; F, funnel-shaped opening of duct.

the dorsal area, the glands occur beneath both the dorso-lateral and dorso-median walls. Further to the posterior where, owing to the asymmetry of the horse-shoe, the ventral setæ are situated near to the median wall of the statocyst, the glands are most numerous beneath the dorso-median wall. Although the glands never lie actually beneath the setæ they do appear to be definitely associated with them because they vary in position quite regularly in accordance with the distribution of the setæ.

The ducts from the glands pass through the tissues and then penetrate the integument. They possess one highly characteristic feature, a wide funnel-shaped opening (Fig. 2, F) at the surface of the integument opening into the cavity of the statocyst. Openings of this type never occur in other regions of the integument where the glands are concerned solely with the production of the bounding cuticle.

4. Nature of the Hyaline Secretion.

A variety of tests corresponding to those employed by Yonge (1932) for the identification of the cuticle and the chitin were applied to the hyaline secretion which secures the sand grains, or statoliths, to the sensory setæ. The nature and results of these tests are outlined in Table I, the statements in columns 2 and 3 being taken from Yonge.

TABLE I.

Test.	Chitin.	Cuticle.	Hyaline Secretion.
Conc. HCl	Dissolves immediately.	Dissolves very slowly.	Dissolves very slowly.
Hot 40% NaOH	Insoluble.	Dissolves immediately.	Dissolves immediately.
Iso-electric point	pH 3·5	pH 5·1	pH 5·1
Mallory	Stains blue.	Stains red.	Stains red.
Sudan III	Not stained.	Stains red.	Stains red.

It will be noted that in every case the reactions of the hyaline secretion are identical with those of the cuticle and different from those of the chitin. The action of NaOH on the secretion is well illustrated by the difference between the appearance of the setæ with adhering sand grains before and after treatment. This is shown in Fig. 4, A and B. Not only has the hyaline secretion disappeared in B, but the setæ have lost their rigid appearance owing to the dissolution of the bounding cuticle which is largely responsible for this. The underlying chitin has not been attacked. There is the same difference between the iso-electric point of the hyaline secretion and that of the chitin as there is between the iso-electric points of the cuticle and the chitin and with the same consequent differences between the staining reactions as exemplified by the anilin blue (basic) and the acid fuchsin of the Mallory. Finally, the action of Sudan III indicates that the lipoid constituent, so characteristic of the cuticle and so all-important in controlling the permeability of the uncalcified integument (Yonge, 1935), is also present in the hyaline secretion.

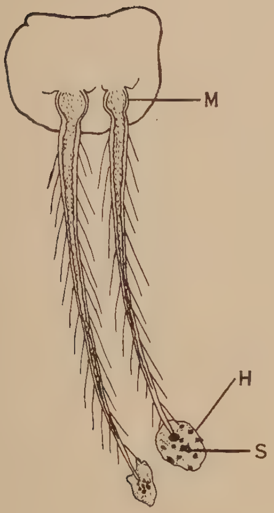

Fig. 3.—Sensory setæ with attached sand grains. ×48. H, hyaline secretion; M, spherical membrane; S, sand grains attached to setæ by hyaline secretion.

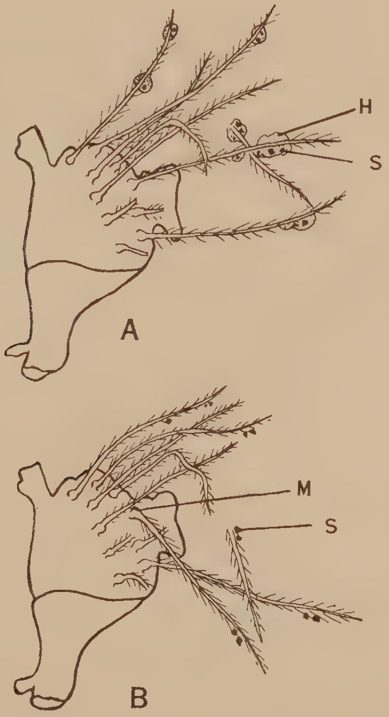

Fig. 4.—Group of setæ with attached sand grains. A, before, and B, after treatment, with hot 40% NaOH. ×24. Other lettering as before.

5. Discussion.

The evidence presented in this paper gives very considerable support to the view of Prentiss that the hyaline substance which secures the statoliths to the setæ in the statocysts of the Decapod Crustacea is secreted by tegumental glands. The most significant data are provided by the reactions of the hyaline secretion which agree in every respect with those of the cuticle. The tegumental glands situated around the statocyst, though they do not occur actually beneath the setæ, are arranged in definite relation to these. They are similar in every respect to those which secrete the bounding cuticle, but this is also true of those which secrete the cement which binds the eggs to the pleopods of the female. The question arises, how is it that the secretion of these glands enters the cavity of the statocyst and there cements the sand grains on to the setæ, and does not spread out over the surface of the integument like the secretion of the great majority of these glands ? The probable explanation is that these particular tegumental glands secrete immediately *after* and not some little time before the actual moult. As shown by Yonge (1932), the tegumental glands which form the cuticle begin to secrete some weeks before the actual moult (in the case of *H. vulgaris*) ; the first indications of the new cuticle being found when the first indications of the gastroliths appear. By the time the old integument is ready to be cast the cuticle (though *not* the underlying chitin) is fully formed and the glands have begun to degenerate. In other words the cuticle is fully formed before it is exposed. Although there is no experimental evidence to support this statement, it is not unreasonable to assume that if these glands poured out their secretion after the moult, so that it was exposed at once to the action of the surrounding sea water, it would not spread over the surface of the integument. Sand grains lying in the cavity of the statocyst would be entangled with this secretion and would adhere to the only projecting objects in the cavity, namely the setæ. The secretion, as in the case of the cuticle and the cement which secures the eggs, quickly sets hard after exposure, and in this way the statoliths would be firmly secured to the sensory setæ. The wide, funnel-like openings of the ducts indicate that the secretion is set free into the cavity of the statocyst as suggested here.

This research is of interest, not only because it lends great support to the theory originally put forward by Prentiss, but because it draws further attention to the great importance of the tegumental glands in the Crustacea ; glands which are unique in having accessory functions almost as important as their primary one.

The authors wish to acknowledge financial assistance received from the Colston Research Fund of the University of Bristol.

6. SUMMARY.

1. The general structure of the statocyst and the combined sensory setæ in *Homarus vulgaris* have been described.

2. The statoliths consist of sand grains attached to the setæ by a hyaline secretion.

3. Numerous tegumental glands occur in the sub-epithelial tissues. Though not situated beneath the setæ, their distribution varies in accordance with that of the setæ. Their ducts have characteristic funnel-shaped endings, opening into the cavity of the statocyst.

4. The hyaline secretion agrees in all its reactions with the cuticle, never with the chitin.

5. The conclusion is reached that the hyaline secretion is formed by these tegumental glands and that this constitutes an important accessory function of these glands.

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On Some Aspects of Digestion in Ciliary Feeding Animals.

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THIS paper embodies various observations which were made from time to time while the author was a member of the staff of the Plymouth Laboratory. It also outlines certain generalisations based on the author's previous published work and that of other recent workers in the field of comparative physiology of feeding and digestion.

Animals which obtain their food by means of ciliary mechanisms are characterised, amongst other things, by (1) a great admixture of mucus with the food, (2) continuous feeding within certain limits of temperature, (3) the almost complete absence of muscle from the gut and so of peristalsis and (4) the possession of firm fæces. It is with these points, in particular, that this paper is concerned.

THE RÔLE OF MUCUS IN FEEDING.

Mucous glands are invariably associated with cilia. In animals which have, as a result of evolutionary processes, to a large extent lost ciliary feeding mechanisms, present in their ancestors, mucous glands are correspondingly reduced in numbers. This is particularly well shown in the Septibranchs (Yonge, 1928). It has been stated by Nicol (1930) that mucus is particularly concerned with the rejection of large particles and plays little, if any, part in the true feeding process. This view cannot be accepted. There are, it is true, a greater number of mucous glands in rejection tracts of cilia but this can be correlated with the larger particles dealt with. The examination of stomach contents in Lamellibranchs and in Tunicates, such as Phallusia, reveals the presence of mucous strings containing food. Orton (1923) speaks of mucous strings in the stomach of Ostrea as being wound round the revolving head of the style "like a capstan."

The question arises, by what means is the mechanical obstruction presented to digestion by the mucus, which encloses the food, overcome ? Orton (1922) suggested that the mucus was digested in Lamellibranchs by an enzyme present in the style. There is abundant evidence (summarised by Yonge, 1930) that there is no protease in the gut of Lamellibranchs, food containing protein being ingested by the wandering phagocytes and, if small enough, in the cells of the digestive diverticula. Nelson (1933) has recently reopened this question by suggesting that the chitinous covering of planktonic Crustacea and the cuticle of Nematodes is disintegrated in the stomach of oysters by enzymes from the style. To test the truth of this statement an extract was made of the styles of 20 *Mya arenaria* (total weight 4 grams) and experiments, with controls, were run for three weeks on portions of the uncalcified chitin of Homarus and of the cuticle of Ascaris. In neither case was any trace of digestion observed.

The solution to the problem appears to lie in the pH of the medium. Mucus is an amphoteric protein the viscosity of which alters with the hydrogen ion concentration of the medium. Mills (1931) carried out viscosity determinations on the mucus from the mouth cavity of *Helix aspersa* and found that there was a well-marked maximum at pH 8·0. It is impossible to obtain sufficient mucus from any ciliary feeding mechanism for viscosity determinations. All that can be done is to obtain mucous strands by the application of fine, clean sand and then determine the iso-electric point of the mucus by the colorimetric method of Loeb (1922). The results of a series of such determinations, together with the hydrogen ion concentration in the stomach of the animals concerned, are given in Table I.

TABLE I.

Animal.	Iso-electric point of mucus.	pH of stomach fluid.
Ostrea edulis	ca. 6·0	5·5
Mytilus edulis . . .	6·3	6·1
Pecten maximus . . .	5·6	5·6
Phallusia mammillata . .	5·6	5·4
Metridium senile . . .	6·4	6·7

It will be seen that in all cases, although the animals belong to three widely different phyla having only ciliary feeding mechanisms as common characters, there is a close agreement between the iso-electric point of the mucus and the hydrogen ion concentration in the stomach. Since the colloidal properties of a protein are at the minimum at the iso-electric point, it follows that viscosity should be lowest here.* The mucus which enters the stomach of these animals will therefore be much less viscous than it was in the region where it was secreted—i.e. in the mantle cavity of the Lamellibranchs, the branchial sac of Phallusia and the surface of the disc and tentacles in Metridium. It is not unreasonable to suppose that this lowered viscosity is of significant importance in assisting the digestive processes.

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* Orton's statement (1922) that the style assists in the dissolution of mucus actually confirms this because it is the acid nature of the style substance which is responsible for the low pH in the stomach of Lamellibranchs (Yonge, 1925, b, 1926).

THE NATURE OF THE FEEDING PROCESSES.

Unlike the majority of other animals, ciliary feeders do not " take meals " from time to time. So long as environmental conditions, the most important of which is temperature, are suitable they feed continuously and mechanically. Since food is continually being passed into the gut, it follows that digestion also must be a *continuous process*. The implications of this have not always been realised. In animals where food is taken in bulk at definite times, the secretion of digestive enzymes is intermittent. There may be a regular rhythm of secretion as there is in Helix (Krijgsman, 1925) and in Astacus (Hirsch & Jacobs, 1928), or secretion may occur in response to stimulation associated with the presence of food in the gut, as in the Vertebrates.

There is, unfortunately, no evidence about the periodicity of secretion in ciliary feeders, apart from the Lamellibranchs. Here the style supplies the only extracellular enzyme and, as pointed out elsewhere (Yonge, 1932), the style constitutes an ideal mechanism for the *continuous liberation of small quantities of enzyme*. The enzyme is secreted in the style-sac and is in all probability adsorbed by the protein matrix of the style. The style is being continually and very slowly pushed forward towards the stomach. There the head end is gradually dissolved away owing to the less acid nature of the fluid in that region (Yonge, 1925, b). Even though there be a periodicity in the actual secretion of the enzyme—and on this point there is no evidence—the *liberation* of the enzyme into the stomach will be continuous. The substance of the style provides an ideal vehicle both for the conveyance and the continuous liberation of the enzyme. It would be interesting to know whether or not there is a periodicity in secretion in the Tunicates, ciliary feeders in which digestion is exclusively extracellular.

Berrill (1929), Graham (1931) and Pantin (1932) have drawn attention to the importance of duration of enzyme action in connexion with the effect of temperature. The longer the duration the lower will be the apparent optimum temperature. They have correlated their findings with the conditions which exist in the animals studied (the Ascidians, *Tethyum pyriforme americanum* and *Boltenia ovifera*, and the Lamellibranch, *Pecten maximus*) and point out that at all normal temperatures the time taken by food to pass through the gut corresponds to the duration of enzyme experiments for which that particular temperature is optimal. These results are of great interest, but it is a little unfortunate that the experiments should all have been carried out on animals with ciliary feeding mechanisms. It is rather questionable whether experiments made with extracts of large numbers of styles or of large quantities of digestive tissues of Ascidians acting on large amounts of substrate have any significant bearing on conditions in animals where a thin but continuous stream of food is subjected to the continous action of minute quantities of enzyme. Moreover, in the case of the Lamellibranchs the time passage through the gut is *no indication* of the effective duration of enzyme action. The greater part of the time spent in passing through the gut is occupied in the mid- and hind-guts in which, as stated below, no absorption takes place. It is noteworthy that Nicol (1930) was unable to obtain similar results with *Sabella pavonina*.

Function of the Mid-gut.

There would seem to be a definite correlation between the length and also the function of the mid-gut and the actual position where the fæces are extruded. This applies also to animals which do not feed by ciliary mechanisms. Graham (1932) has pointed out, with excellent evidence, that the very long coiled gut in *Patella vulgaris* is probably concerned exclusively with the formation of firm fæces. It is very necessary that an animal which discharges its fæces into the mantle cavity should avoid the fouling which would ensue were these extruded in a loose or particulate condition. Absorption does not take place in the mid-gut of Lamellibranchs and many (possibly all) Gastropods, this region being concerned with the preliminary moulding of the fæces, a slow process in animals where material is moved through the gut by ciliary instead of muscular action.

Absorption does occur in the mid-gut of the Ascidians (Yonge, 1925, a) which is also ciliated and without muscle, but in this case there is no danger of the fæces fouling the collecting mechanism. The mid-gut in this case is very short. In the Septibranchs also (which are exceptions to every rule in the Lamellibranchs) the mid-gut is a straight tube leading directly from the stomach to the hind-gut. But here the collecting mechanism is muscular and not ciliary, and so unlikely to be fouled, and moreover the food consists of large masses and not of finely divided particles which need to be massed together. In the ciliary feeding Annelids such as Sabella, the gut is a straight tube, but the anus is situated at the posterior end, as far removed as possible from the collecting mechanism.

Formation of Fæces.

The firmness and characteristic shape of the fæcal pellets of a variety of invertebrates has been very well demonstrated by Moore in a series of papers (1931, a, 1931, b, 1932, a, 1932, b). In the Crustacea where the mid- and hind-guts are very muscular it is not difficult to see how these pellets have been consolidated and moulded. The necessity for a preliminary moulding in the elongated mid-gut of many ciliary feeders has just been commented upon. The final process takes place in the hind-gut. In all animals of this type which the author has studied the hind-gut is characterised by the presence of muscle, especially near the anus, and also by great accumulations of mucous glands. This also appears to be true for Patella and Sabella. If the low pH of the fluid in the stomach is of importance in lowering the viscosity of the mucus, one would expect to find exactly the reverse in the hind-gut where maximum viscosity is needed. This is actually the case. As recorded elsewhere (Yonge, 1925, b, 1926), the pH in the hind-gut is higher than in any other part of the gut in both Lamellibranchs and Gastropods. In Phallusia where the pH in the stomach is about 5·4, that of the hind-gut is about 7·1. It appears not unreasonable to assume that this high pH is of value to these animals by increasing the viscosity of the mucus and thereby assisting in the consolidation of the fæces.

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Studies on Conditioned Responses in Fishes. Part III. Wave-length Discrimination in *Blennius pholis* L.

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1. Introduction.

It has been shown (**1**, **2**) that the capacity for building up visual conditioned responses is common to many types of fish when the unconditioned stimulus used as the basis for the "conditioning" is *food*. Preliminary work at Plymouth, using the fish *Blennius gattorugine*, showed that it was possible that a knowledge of wave-length discrimination in that species might be acquired by the now familiar method of "conditioning" to an *electric shock*. This work was continued when I came to Cullercoats, and six specimens were used which were sent from Plymouth in 1929. All of these died within a short space of time during the succeeding winter months, owing to the intense cold. It was therefore necessary to restrict the investigation to *Blennius pholis L.*, which is both plentiful and hardy at Cullercoats. Some progress had already been made and in Part II (**2**) it was intimated that an analysis would be made of the capacity for wave-length discrimination in *Blennius pholis* using an electric shock as the unconditioned stimulus. The present paper gives the results of that enquiry as far as it was taken.

The motor response to the electric shock is probably of a truly reflex nature. The responses involved in food-taking are more complex and probably not of the nature of reflexes. This enquiry was thus originally begun with the object of ascertaining primarily whether this type of experiment (use of electric shock) was more likely to yield reliable information upon sensory discrimination than that where the unconditioned stimulus was food. The range of wave-lengths investigated is therefore more restricted than it would have been had the investigation into wave-length discrimination been the sole objective. Sufficient ground was covered, however, to show a very wide range of wave-length discrimination in this fish.

In order to establish the evidence of capacity for wave-length discrimination in fishes the light-stimulus must be presented in such a way as to eliminate the possibility that intensity, shape, form, or any other kind of environmental change is being associated with the shock. The intensity factor has been controlled and virtually eliminated in the present investigation by demonstrating that after discrimination has been effected it continues to be shown at varying intensities obtained by raising and lowering the source of light in a closed " light " box as described in more detail below. In the earlier parts of these studies it was found simple and convenient to represent the whole course of an experiment graphically. The general course of learning in these fishes was thus readily portrayed. It is not possible to do this in the present instance in such a way as to illustrate the essential feature involved, i.e. differentiation between one or more wave-lengths and their varying intensities. Owing to the prohibitive cost of printing the detailed histories of these experiments it has been necessary to restrict the detail to one typical " log," and merely to summarise in the present paper the salient features of the remaining experiments in regard to wave-length discrimination. While the results of the different experiments are in general agreement, no two individuals can be said to have reacted identically, although their recorded response was reduced to the simplest possible form—the presence or absence of a bodily movement. Each individual had not only some physical feature rendering it familiar as an individual, but had recognisable idiosyncrasies relating to its general behaviour. General notes relating to the method, the scope of the inquiry, and its relations to wider problems are to be found in Part I (**1**).

II. Procedure.

The methods used have been described in an earlier paper (**1**) and remain unchanged in their essential arrangement.

Visual stimuli of varying wave-length were obtained by the use of Wratten gelatine light-filters in conjunction with a " Stella " 100 w. tungsten filament gas-filled opal lamp operating on a 240-volt alternating current supply. The lamp was housed in a " light chamber," an elongated box 50 inches long and 5 inches square in section, with a dead-black smooth interior surface. The lamp was held by a string passing over the top of the "light chamber," by which it could be raised or lowered, the extent of which movement was measured by a scale on the outside of the box. The lower end of the box was closed by a smooth-running lantern-slide carrier accommodating the filters. These were obtained from Kodak Ltd. in the form of plain gelatine films and were then suitably mounted between two cover-glasses of selected quality. The characteristics of the filters used are tabulated in Table I, taken from the Eastman Kodak Co.'s book on "Light filters." The total transmissions are accurate to within 5%, with the exception of Neutral Grey No. 96, which is accurate to within 10%. Under the conditions of these experiments it is unnecessary to calibrate more accurately.

A diffusing screen was placed within the light chamber immediately above the colour filter. This was a fixture throughout the series. The "light chamber" was set up in position over the cabinet housing the fish undergoing "conditioning" so as to be immediately dorsal to a circular opening of 1·5 inches in diameter in the top of the cabinet. The actual visual stimulus as presented to the fish in the vessel within the cabinet was therefore a circle of light immediately above it.

The general disposition of the remaining parts was as described in Part I (**1**), p. 525. The light and the shock were operated from soft copper knife switches placed at 4 feet distance on thick felt on a separate stand. Disturbances were eliminated as far as possible by carrying out the experiments on the dark-adapted fishes at night; by doing those on daylight-adapted individuals in a locked room; and by covering the floor and the various stands with thick felt. In addition, care was taken to reduce personal activity to a minimum during the course of an actual stimulation. The cabinet housing the fish was light proof when closed for the experiments on dark-adapted individuals. The response was noted by means of a pointer connected to a cover-glass treated so that it floated on the top of the water containing the fish, as described in Part I, p. 525. Movement of the pointer was observed against a white background faintly illuminated by a small electric torch.

The filters chosen for the work on each individual were generally of a closely similar total transmission, in order to avoid any considerable intensity differences from the beginning. It is, however, practically certain that under the conditions of the experiment, very wide differences in intensity can probably be permitted without affecting the issue relating to wave-length discrimination. In this respect they contrast strongly with experiments involving a choice between two contiguous colours or coloured surfaces, or those where a preference is apparently exhibited between coloured compartments, etc. There is, in addition, direct proof in one of the present experiments that this fish does not differentiate

TABLE I.

[By permission of Eastman Kodak Co.]

PHYSICAL CHARACTERISTICS OF THE FILTERS USED IN THESE EXPERIMENTS.

These particulars are those of the makers. The names and the numbers are taken from their catalogue. Immediately beneath the filter number is the approximate value of the total light transmission of each filter (percentage). The columns below this give the percentage transmissions of the light of the wave-length values indicated in the first vertical column, where the wave-lengths are shown in millimicrons. The values given throughout are those for the maker's standard films: particular filters are liable to diverge somewhat from these figures.

Colour of filter	Red	Magenta	Blue	Green	Red	Orange-red	Orange-yellow	Yellow-green	Pure green	Blue-green	Neutra grey
Name of filter	Stage red	Minus green	Dark toluidine blue	B_2	α	β	γ	δ	ϵ	η	—
No. of filter	27	32	38A	58	70	71A	72	73	74	75	96
Total transmission	23·0	19·0	16·5	23·0	0·6	1·0	1·0	3·3	3·3	1·5	various
Wave length mμ											
400	—	42·80	33·80	—	—	—	—	—	—	—	6·72
10	—	47·90	38·90	—	—	—	—	—	—	—	7·58
20	—	53·60	43·50	—	—	—	—	—	—	—	7·96
30	—	60·10	46·60	—	—	—	—	—	—	—	8·12
40	—	65·10	49·00	—	—	—	—	—	—	—	8·12
50	—	63·10	49·60	—	—	—	—	—	—	—	7·96
60	—	52·80	50·10	—	—	—	—	—	—	0·80	7·85
70	—	40·00	49·00	—	—	—	—	—	—	6·30	7·58
80	—	26·40	46·90	1·97	—	—	—	—	—	17·30	7·43
90	—	13·80	43·50	11·46	—	—	—	—	—	19·10	7·23
500	—	3·99	39·70	30·23	—	—	—	—	—	14·10	7·23
10	—	0·62	36·60	50·10	—	—	—	—	1·00	5·00	7·23
20	—	—	31·60	60·20	—	—	—	—	8·00	1·30	7·23
30	—	—	27·60	54·70	—	—	—	—	15·10	0·31	7·58
40	—	—	73·60	39·00	—	—	—	—	10·00	—	7·85
50	—	—	19·50	30·20	—	—	—	—	4·00	—	7·96
60	—	—	15·00	25·10	—	—	—	2·50	1·14	—	8·12
70	—	—	11·70	17·00	—	—	—	8·00	0·12	—	8·12
80	1·26	—	8·30	10·00	—	—	—	5·70	—	—	8·12
90	33·00	—	5·60	5·50	—	—	1·14	2·68	—	—	7·96
600	61·90	—	3·70	2·80	—	—	3·78	1·10	—	—	7·58
10	78·30	3·00	2·30	1·30	—	1·26	4·40	0·39	—	—	7·23
20	78·30	39·60	1·50	0·57	—	7·10	2·86	0·15	—	—	7·08
30	78·30	67·50	0·96	0·21	—	9·80	1·51	—	—	—	6·93
40	78·30	79·40	0·62	—	—	10·00	0·78	—	—	—	6·93
50	78·30	79·40	0·52	—	1·00	9·20	0·37	—	—	—	6·93
60	78·30	79·40	0·42	—	10·00	8·00	0·37	—	—	—	6·93
70	78·30	79·40	0·40	—	25·10	7·10	0·49	—	—	—	7·23
80	78·30	79·40	0·39	—	39·80	6·60	1·24	0·15	—	—	7·30
90	78·30	79·40	0·38	0·10	57·60	6·70	3·78	2·18	—	0·10	7·58
700	79·40	79·40	0·37	0·73	74·50	8·00	11·50	6·30	—	0·24	7·85

between very wide differences in intensity of grey. Apart from this, the intensity factor was eliminated by adjustment of the height of the lamp above the diffusing screen at successive trials in such a way that the colour being discriminated was at times relatively brighter or duller than the primary conditioning stimulus and passed through all intermediate conditions.

A standard scale of distances of the several parts of the lighting arrangement was adopted for the primary conditioning colour in each instance. This intensity is spoken of as " threshold " intensity throughout, and was equivalent at the point where the filter interrupted the light to an illumination of approx. 10,000 metre-candles.

With two exceptions (specimens A and B) the routine of the *daily* procedure was the same throughout. The specimen was taken from the laboratory tanks and placed carefully in the experimental apparatus at an interval varying from 15 to 60 minutes before the first " signalling " stimulus of the day. It was then given a succession of " signalling " stimuli, usually at intervals of 5 minutes. The number of these ranged from 5 to 10 per day. After a further interval of not less than 15 minutes the fish was taken out and returned to its normal environment in the laboratory tanks. At the same time if more than one was being investigated, another fish was placed in the apparatus, and so on until the daily routine was completed. In the early stages of each individual's record the " signalling " stimulus was constantly associated with an electric shock given shortly after. Such stimuli were, therefore, " conditioning " stimuli. After a number of such associations these stimuli were found by themselves to evoke the bodily movement originally associated with the shock. Thus a conditioned response was established.

A second " signalling " stimulus with different optical properties was then introduced in irregular sequence, but at no time was this one associated with a succeeding shock. The light was allowed to act for the whole of the interval between " signalling " and " shock " when using the conditioning stimulus, and for one minute or longer when using the contrasting stimulus. (All presentations of the contrasting stimulus are *italicised* in the representative table.)

All the specimens used were of full adult size.

Different wave-lengths were used for the discriminations in each one of the individuals used. The fish were known by a distinctive letter and the results are summarised for convenience under these letters. The summaries show the full nature of the wave-length discriminations investigated, and give the salient features relating to this point. A detailed record of one of the experiments as a typical example of procedure is given in the next section, and all are summarised in Section IV.

The full records of the experiments will be deposited in the British

Museum (Natural History) in accordance with the scheme for the deposition of lengthy tabular matter too extensive for complete publication. They may be consulted there on application to the Director, British Museum (Natural History), South Kensington, London, S.W. 7.

III. DETAILED RECORD OF AN EXPERIMENT ON A DARK-ADAPTED FISH ILLUSTRATING THE GENERAL NATURE OF THE EXPERIMENTS AND THE PROGRESS OF "CONDITIONING" AND SUBSEQUENT "DIFFERENTIAL DISCRIMINATION."

This typical record (Table II) shows the details of the experiment where one intensity of grey was used for conditioning, and subsequent discrimination was studied for other intensities of grey. It has already been shown that *Labrus bergylta* (**1**, pp. 513-9) does not discriminate comparatively wide differences in intensity of a light source. *Blennius pholis* and *Labrus bergylta* both predominantly seek for food, etc., by sight so far as may be ascertained by ordinary observation of their behaviour. A demonstration that *Blennius pholis* likewise could not discriminate between wide differences in intensity would support any positive evidence of wave-length discrimination which might be derived from other experiments in this series, regardless of any precaution which might have been actually taken to ensure that intensity was not the discriminated factor. The record shows conclusively that this is actually so. The fish was positively conditioned to Neutral Grey (No. 96), with a total transmission of 25%, and with the light at "zero" position ("Threshold" intensity as defined on p. 351). This is equivalent to an intensity of approximately 20,000 metre-candles at the diffusing screen. This conditioning stimulus preceded the shock by 2 seconds. The detailed "log" is shown in Table II.

A suggestion of "conditioning" appeared at the 25th–28th trials (Dec. 16th), but no further evidence of it was seen until the 75th trial on January 14th, from which date it remained constant. It may be noted that during the period December 21st to January 8th no experiments were made. From January 15th onwards this fish was given repeated trials (interspersed with typical conditioning) of a number of other intensities of grey. These were obtained as already stated by raising the light source to varying heights above the diffusing screen, and are all italicised in the table (i.e. trials No. 82, 85, 87, Jan. 15th). It will be seen that throughout the remainder of the investigation on this fish all intensities down to (0·0017 × Threshold) evoked fairly uniformly a sharp motor response differing in no apparent respect from the conditioned response elicited by the primary conditioning intensity. Absence of movement occurred consistently only with an intensity of 0·00098 × Threshold, which is equivalent to approximately 20 metre-candles.

It appears certain, therefore, that under the conditions of these experiments *Blennius pholis* cannot discriminate such small intensity differences as exist between the colour filters used in the other individuals. The reason for the insistence on this point is the more readily appreciated by confining oneself in a dark room and attempting to state the comparative brightness of the same circle of light produced under the same conditions.

This is found to be extremely difficult, whilst the colours used in these experiments are readily distinguished as such by human beings with normal vision, regardless of enormous variations in intensity.

It needs to be emphasised that Table II is more than a mere catalogue of experiments similarly performed on the same animal, but at different times. It portrays the orderly development of a conditioned motor reaction in response to the stimulus of a grey light signal ; it then demonstrates that when this is firmly established a great reduction in the intensity of the light signal has no effect on the appearance of the response beyond the fact that if a large number of trials are made without succeeding shock (as at trials 154 to 159), the original response to the primary conditioning stimulus may be weakened. In such an instance a single reinforcement is sufficient to cause its return to its original strength.

IV. NOTES AND SUMMARIES OF EXPERIMENTS ON INDIVIDUAL FISHES IN EACH OF WHICH A DIFFERENT DISCRIMINATION WAS INVESTIGATED.

(a) Dark-adapted fishes.

Specimen A. The Discrimination of unfiltered " white " light from green.*

It has been already stated that the general routine of these experiments was to take the fishes out of the aquarium tanks some time before a series of conditioning trials and to replace them after the day's work. This specimen (as also was Specimen B) was confined to the completely dark apparatus for the duration of the whole experiment, from March 12th to May 22nd. The fishes lived apparently healthily and contentedly and it was noted that they took food on occasion at the same time as a shock was given, thus showing its relatively innocuous nature.

The primary conditioning stimulus was Wratten filter No. 58, B2, green, transmitting mainly 490–580mμ, with a total transmission of 23%, preceding the shock by 3 seconds.

The fish was given no visual stimuli until April 6th. It was then thoroughly tested with the green light alone, unaccompanied by shock,

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* The colour of the light of a tungsten filament gas-filled opal lamp whilst ordinarily spoken of as " white " has in fact a saturation of 56%, and a " hue " of approximately 586 mμ.

TABLE II.

"Log" of Experiment on Specimen F. (*Blennius pholis*).

The columns in order from left to right show :

1. Date and times when specimen was put into the apparatus (the first-mentioned) and taken out again at the conclusion of each day's work (the last-mentioned) ; the times in brackets. Continental timing throughout (24-hour system).
2. The times of each association or trial.
3. The serial number of each association or trial.
4. Nature of the stimulus used. The positive "conditioning" stimulus for the establishing of the conditioned response was Neutral Grey, filter No. 96 used at "zero" distance from the screen as explained in text (p. 351). This is called "Threshold," and all trials with this are shown in plain type.
   The differential stimuli of lower intensities of grey are shown as fractions of the primary intensity, and all such trials are shown in italics.
5. The nature of the response to the stimulus named in 4.
6. The shock-reaction. This is noted to show that upon each occasion of giving the positive stimulus, a shock followed and caused a reaction (except for occasional trials when no shock was given for test purposes) ; all the intensities below threshold were not followed by shock, and the note is made "No S. given."

1.	2.	3.	4.	5.	6.
Date. Times when put in and taken out of apparatus.	Time of each trial.	Number of trial.	Nature of signalling stimulus. T.=Threshold.	Resultant movement to 1. Signalling stimulus.	Resultant movement to 2. Shock. S.=Shock. R.=Response.
Dec. 9 [**18** 50 ; **19** 40]	**19** 05, 08, 11, 14, 17, 20, 25, 30	1 to 8	Grey. T.	None	Strong R.
Dec. 10–11. No expts.					
Dec. 12 [**17** 00 ; **17** 36]	**17** 17, 20, 23, 26, 28, 31	9 to 14	,,	,,	,,
Dec. 13. No expts.					
Dec. 14 [**21** 20 ; **21** 45]	**21** 30, 32, 34, 36, 38, 40, 42	15 to 21	,,	,,	,,
Dec. 15. No expts.					
Dec. 16 [**20** 40 ; **21** 20]	**20** 53, 56 ; **21** 00	22 to 24	,,	,,	,,
	21 03	25	,,	Distinct at 1·5″	,,
	21 06	26	,,	,, ,,	,,
	21 10	27	,,	None	,,
	21 12	28	,,	Sharp at 1·5″	,,
Dec. 17. No expts.					
Dec. 18 [**17** 05 ; **17** 56]	**17** 20, 23, 26, 30, 34, 38, 42, 46	29 to 36	,,	None	,,
Dec. 19 [**21** 05 ; **22** 10]	**21** 20, 25, 28, 30, 35, 40, 45, 50, **22** 00	37 to 46	,,	,,	,,
Dec. 20 [**18** 25 ; **19** 30]	**18** 40, 43, 46, 50, 55 ; **19** 00, 03, 06, 10, 15	47 to 56	,,	,,	,,
Dec. 21 to Jan. 8. No expts.					
Jan. 9 [**16** 55 ; **18** 00]	**17** 10, 15, 20, 25, 30, 35, 40, 45	57 to 64	,,	,,	,,
Jan. 10–12. No expts.					
Jan. 13 [**21** 00 ; **22** 00]	**21** 15, 20, 25, 30, 35, 40, 45	65 to 71	,,	,,	,,
Jan. 14 [**21** 05 ; **22** 50]	**21** 20, 25, 30	72 to 74	,,	,,	,,
	21 35	75	,,	Strong at once	,,
	21 40	76	,,	,, ,,	,,
	21 45	77	,,	,, 1·2″	,,
	21 50	78	,,	,, once	,,
	22 20	79	,,	,, ,,	,,
Jan. 15 [**18** 35 ; **19** 40]	**18** 50, 55	80, 81	,,	,, 1·8″	,,
	19 00	*82*	*0·00098 T.*	*None in 30″*	*No S. given.*
	19 05	83	T.	Strong at once	Strong R.
	19 10	84	,,	,, 1″	No S. given.
	19 15	*85*	*0·0039 T.*	*None in 30″*	*No S. given.*
	19 20	86	T.	Strong at once	Strong R.
	19 25	*87*	*0·0156 T.*	*Strong at 0·8″*	*No S. given.*
Jan. 16–19. No expts.					
Jan. 20 [**16** 00 ; **16** 55]	**16** 15	88	T.	None in 2″	Strong R.
	16 20	89	,,	Strong at once	,,
	16 25	90	,,	,, 1·6″	,,
	16 30	*91*	*0·00098 T.*	*None in 30″*	*No S. given.*
	16 35	*92*	*0·0039 T.*	*Strong at 3″*	,,
	16 40	93	T.	Strong at 1·2″	Strong R.
Jan. 21 [**21** 25 ; **22** 10]	**21** 40, 45	94, 95	,,	,, once	,,
	21 50	*96*	*0·00098 T.*	*None in 30″*	*No S. given.*
	21 55	*97*	*0·0039 T.*	*Strong at once*	,,
	22 00	98	T.	,, ,,	Strong R.

1. Date. Times when put in and taken out of apparatus.	2. Time of each trial.	3. Number of trial.	4. Nature of signalling stimulus. T. = Threshold.	5. Resultant movement to 1. Signalling stimulus.	6. 2. Shock. S. = Shock. R. = Response.
Jan. 22. No expts.					
Jan. 23 [**20** 35 ; **21** 35]	**20** 45	99	T.	None in 2″	Strong R.
	20 50	100	,,	Strong at 2·2″	No S. given.
	20 55	101	*0·25 T.*	*Strong at 3·0″*	*No S. given.*
	21 00	*102*	*0·0625 T.*	,, *1·2″*	,,
	21 05	*103*	*0·0278 T.*	,, *0·2″*	,,
	21 10	104	T.	Strong at 1·6″	Strong R.
	21 15	*105*	*0·00098 T.*	*None in 30″*	*No S. given.*
Jan. 24 [**18** 00 ; **19** 00]	**18** 25	*106*	*0·00098 T.*	*Strong at once*	,,
	18 30	107	T.	None in 2″	No S. given.
	18 35	108	,,	Slight at 0·2″	Strong R.
	18 40, 45	109, 110	,,	Strong at once	,,
Jan. 25. No expts.					
Jan. 26 [**18** 45 ; **19** 45]	**19** 05	111	,,	,, 0·4″	,,
	19 10	*112*	*0·0156 T.*	,, *once*	*No S. given.*
	19 15	*113*	*0·00098 T.*	*None in 30″*	,,
	19 20	*114*	,,	,, ,,	,,
	19 25	*115*	*0·0625 T.*	*Strong at 1·4″*	,,
	19 30	116	T.	Strong at 1·8″	Strong R.
Jan. 27 [**18** 35 ; **19** 40]	**19** 00	117	,,	,, once	,,
	19 05	*118*	*0·00098 T.*	*None in 30″*	*No S. given.*
	19 10	*119*	*0·0156 T.*	*Strong at 1·6″*	,,
	19 15	*120*	*0·0039 T.*	*Distinct at once*	,,
	19 20	121	T.	Distinct at once	Strong R.
Jan. 28 [**20** 20 ; **21** 05]	**20** 40	*122*	*0·00098 T.*	*None in 30″*	*No S. given.*
	20 45	123	T.	Strong at once	Strong R.
	20 50	*124*	*0·00098 T.*	*None in 30″*	*No S. given.*
	20 55	*125*	*0·0039 T.*	*Distinct at 5.″*	,,
	21 00	126	T.	Strong at 0·8″	,,
	21 05	127	,,	,, 1·2″	Strong R.
Jan. 29. No expts.					
Jan. 30 [**19** 02 ; **20** 05]	**19** 30	*128*	*0·0156 T.*	*Sharp at once.*	*No S. given.*
	19 35	*129*	*0·00098 T.*	*None in 30″*	,,
	19 40	130	T.	Strong at once.	,,
	19 45	131	,,	,, ,,	Strong R.
Jan. 31 [**19** 35 ; **20** 40]	**19** 50	132	,,	,, ,,	No S. given.
	19 55	133	,,	,, 1·4″	Strong R.
	20 00	*134*	*0·00098 T.*	*None in 30″*	*No S. given.*
	20 05	*135*	*0·0039 T.*	*Sharp at once*	,,
	20 10	*136*	*0·00098 T.*	*None in 30″*	,,
	20 15	*137*	*0·0039 T.*	*Distinct at 2″*	,,
	20 20	138	T.	,, ,,	,,
	20 25	139	,,	Strong at 2″	Strong R.
Feb. 1, 2. No expts.					
Feb. 3 [**18** 40 ; **19** 40)	**18** 50	*140*	*0·0039 T.*	*Sharp at once*	*No S. given.*
	18 55	141	T.	Strong at 0·8″	Strong R.
	19 00	*142*	*0·0039 T.*	*Strong at 1·4″*	*No S. given.*
	19 05	*143*	*0·00098 T.*	*None in 30″*	,,
	19 10	144	T.	Strong at once	Strong R.
	19 15	*145*	*0·0017 T.*	*Distinct at 3″*	*No S. given.*
	19 20	*146*	*0·00098 T.*	*None in 30″*	,,
	19 25	147	T.	Strong at once	Strong R.
Feb. 4 [**20** 00 ; **21** 30]	**20** 25	*148*	*0·0039 T.*	,, ,,	*No S. given.*
	20 35	*149*	*0·00098 T.*	*None in 30″*	,,
	20 45	150	T.	Strong at 0·6″	Strong R.
	21 00	*151*	*0·0039 T.*	*Strong at 0·6″*	*No S. given.*
Feb. 5 [**20** 05 ; **21** 20]	**20** 20	*152*	*0·00098 T.*	*None in 30″*	,,
	20 25	153	T.	Strong at once	Strong R.
	20 30	*154*	*0·0625 T.*	*Strong at once*	*No S. given.*
	20 35	*155*	*0·0156 T.*	,, ,,	,,
	20 45	*156*	*0·0039 T.*	,, ,,	,,
	20 50	*157*	*0·00098 T.*	*None in 30″*	,,
	20 55	*158*	*0·0039 T.*	*Distinct at once*	,,
	21 00	159	T.	Sharp at once	,,
	21 05	160	,,	None in 2″	Strong R.
	21 10	161	,,	Strong at once	No S. given.
Feb. 6 [**23** 05 ; **00** 05]	**23** 20	162	,,	,, ,,	,,
	23 25	163	,,	,, ,,	Strong R.
	23 30	*164*	*0·0039 T.*	*Strong at once*	*No S. given.*
	23 35	*165*	*0·00098 T.*	*None in 30″*	,,
	23 40	*166*	*0·0017 T.*	*Leisurely at 20″*	,,
	23 45	*167*	*0·0039 T.*	*Sharp at 5.″*	,,
	23 50	168	T.	Sharp at once	No S. given.
Feb. 8. Accidental death of animal.					

at irregular intervals between the hours of 20 00 and 21 30 on April 6th; and between three similar intervals on the three succeeding days; for a total of 50 such trials. No movement occurred in response to any of these presentations. These preliminary presentations were made in all these experiments, and no further specific mention of them is made.

The association of light with succeeding shock was begun on April 10th. Eighty-nine such associated presentations were required before the appearance of a conditioned motor response. This occupied a period of 14 days of actual experiment in a total of 27 days, with an average of 6·7 trials per day of actual experiment. At trial 105 the differential stimulus of unfiltered " white " light unadjusted for intensity was allowed to act for 2 minutes, without succeeding shock. No movement resulted. The same result was obtained with each presentation of the unfiltered light until the conclusion of the experiment at the 183rd trial on May 22nd, regardless of the intensity which was on occasions equated and at times varied considerably.

This fish showed a complete discrimination between the green light and a wide range of intensities of unfiltered " white " light without the necessity for differential conditioning.

Specimen B. The discrimination of unfiltered " white " light from magenta.

The conditions for this individual were the same as those for Specimen A. The primary conditioning stimulus was Wratten filter No. 32 (Minus Green 3), transmitting from 400–500 and 600–700mμ, with a total transmission of 19%, and, as in A, preceded the shock by 3 seconds.

The fish was placed in the apparatus on May 13th and fed and tended, without experiments of any kind until June 1st. After preliminary tests, conditioning was begun on June 4th. A well-defined conditioned motor response was first obtained in response to the magenta light at the 21st trial on the 3rd day of actual experiment. The differential stimulus of " no filter " was first given after the 31st primary conditioning association, and as in Specimen A produced no resultant movement, either during the 2 minutes for which it was allowed to act or during the succeeding 3 minutes of darkness before the next trial. No conditioned movement was obtained with " no filter " at any time in the whole course of the experiment, which was concluded after 103 associations on June 21st. The conclusion was premature owing to the accidental death of the animal, but this fish showed a complete discrimination of the unfiltered light from the magenta regardless of intensity from the commencement, and, as in A, no differential conditioning was required to establish it.

Specimen C. The discrimination of magenta from red.

Primary conditioning stimulus the same as for B, i.e. Wratten filter No. 32, preceding the shock by 5 seconds. Conditioning was begun on December 5th and the experiment concluded on January 21st after 132 trials.

Movement in response to the conditioning stimulus occurred erratically in the earlier stages, isolated responses being elicited at the 15th, 26th, and 47th trials; more certain indications of conditioning occurred on the 12th day at trials 54, 55, 56, and again on the following day at the 64th and 65th; trials 72 to 75 gave positive responses, but the following three negative. From the 79th trial to the conclusion a typical conditioned motor response followed every presentation of the "magenta" colour stimulus. Wratten filter No. 27 (Stage Red), transmitting 580–700mμ, with a total transmission of 23%, was first given at trial 83 as a differential stimulus not followed by shock. At the first three presentations with this stimulus an immediate strong response was recorded apparently differing in no respect from that which was being constantly elicited by the magenta light. At the succeeding trial (86) no movement occurred and from then until the conclusion magenta was uniformly discriminated from red, the former constantly eliciting response, the latter producing no response. The total transmission of these two filters is closely alike (19% and 23%); any difference in intensity resulting from this slight difference may be safely ignored in the circumstances of these tests. Nevertheless, slight variations in intensity were made in order to eliminate this possibility.

Specimen D. The capacity for discrimination of red from magenta, grey, and blue, neutral grey from red and blue, and monochromatic orange-red from orange-yellow.

Several aspects of the conditioning process were investigated in this individual. In the first part, from December 12th to January 21st, the objective and procedure was similar to that of the preceding specimens The fish was positively conditioned to filter No. 27 (Stage Red). The conditioning began on December 12th, the light preceding the shock by 2 seconds. Sharp and immediate movement in response to the conditioning colour first appeared at the 21st trial on the 3rd day of actual experiment. From then until the 84th trial (January 13th) it was elicited fairly consistently. There were no experiments between December 21st and January 12th, a total of 23 days. On resuming on January 13th the first two trials failed to produce a response, but the succeeding trials showed a positive result indicating the stability of the response over the period of absence. Discrimination between the positive conditioning stimulus and the differential stimuli of grey, magenta, and blue, was also shown during this period. From the 85th trial (January 15th) to the 103rd trial (January 20th) the response to the positive conditioning stimulus was, however, very erratic and failed to appear on most of the occasions when it was presented. This was definitely correlated with the fact that the fish was a female with rapidly maturing gonads at the time the experiment began and that the eggs were laid on January 17th. The effect of pregnancy on these responses was repeatedly noticed in Part 1 of these studies. When the fish had recovered and was again feeding readily the conditioned response regained its previous strength and constancy. In the first portion it was established that although the primary conditioning stimulus itself was erratic in its results owing to the reasons mentioned, there was good evidence of discrimination between this and the following :—

Magenta.	Wratten filter 32, particulars in preceding sections.
Grey.	Wratten filter 96, transmitting from 400–700mμ, with a total transmission of 25%.
Blue.	Wratten filter 38A, transmitting mainly 400-550mμ, with a total transmission of 16·5%.

In the second portion, lasting from January 23rd to February 13th, the possibility was investigated of forming a conditioned response to two separate colours over the same period. For this purpose the original conditioning stimulus of Part 1 (Stage Red) was continued, and on no occasion failed to evoke a positive response. For the second colour Dark Toluidine Blue (38A) was used, which, although it had inhibitory properties in Part 1, readily came to act as a second conditioning stimulus. This dual procedure appears to have exercised considerable influence over the capacity to discriminate other colours. Magenta (32), which was still given constantly without a succeeding shock, uniformly evoked a positive response. Neutral Grey (No. 96), previously also "inhibitory," evoked a positive response at 12 out of 29 presentations. But to consider these figures solely as totalities is misleading, and reference should be made to the full tabular history.

It is necessary in each instance to study each day's record carefully, as in the following example from this time.

Record of February 12th (column headings and explanations as in Table II).

1.	2.	3.	4.	5.	6.
Feb. 12 [22 25 ; 23 30]	*22 40*	*121*	*Grey (No. 96)*	*None in 15"*	*No S. given.*
	22 *45*	122	Blue (No. 38A)	Strong at once	,, ,,
	22 50	123	,, ,,	,, ,,	Strong R.
	22 55	124	Red (No. 27)	,, ,,	,, ,,
	23 00	*125*	*Grey* (No. 96)	*None in 15"*	*No S. given.*
	23 05	126	Red (No. 27)	Strong at once	,, ,,

Blue and red were the positive stimuli and grey was the discriminated stimulus which was never followed by shock. The primary object of this part was, however, not concerned with wave-length discrimination, and the matter was not further investigated.

Between February 13th and April 13th, a total of 60 days, no further tests were made with this fish. On starting again, only 11 trials were required to evoke the conditioned response to the blue, while to the more firmly established stimulus of " Stage Red," the response was evoked at its first presentation on April 16th, showing a retention for 63 days.

After this brief test for retention of the conditioned response, a further discrimination was attempted with two colours of much lower intensity and more restricted wave-length. Orange-red, monochromat (filter 71β), 620–700mμ was used as the primary stimulus, with shock following at 3 seconds interval. Nine associations were required to evoke a conditioned response. At the 26th trial, orange-yellow monochromat (filter 72 γ) was introduced, at no time reinforced. At its first presentation it gave a positive response similar to that given to filter 71. After 5 such positive reactions it produced consistently negative responses up to the conclusion of the experiment, showing a very clear evidence of discrimination between these two closely allied regions of the spectrum.

Specimen E. The discrimination of blue from magenta and grey.

This fish was a large female carrying eggs and in similar condition to Specimen D. The conditioning stimulus was Dark Toluidine Blue, filter 38A, transmitting mainly from 400–550mμ, with a total transmission of 16·5%. For the first 130 associations this was given at an interval of one second before the shock. Motor response, apparently " conditioned " in nature, first appeared at the 31st trial on the 4th day of actual experiment, but it remained erratic in appearance. This was found to be due to the superimposition of the response to the shock upon the incipient true conditioned response, so that the latter could not be seen as such. From the 131st trial onwards the interval between stimulus and shock was lengthened to 3 seconds, and no further difficulty occurred.

The discriminating stimuli were magenta, filter 32, and Neutral Grey, filter 96, these being allowed to act for periods varying from 5 seconds to 120 seconds. Particular attention was paid in this specimen to the possibility of movement occurring after these stimuli ceased to act. This was not found to occur.

Both the magenta and grey were discriminated from the blue with exceptional clearness, grey being presented 27 and magenta 37 times during the course of the total of 217 trials covering the period December 12th to February 11th. With each of these colours a positive response was only given at the first presentation ; thereafter they were ineffective.

As in Specimen D some disturbance in the course of conditioning was correlated with the deposition of eggs, but was much less marked.

A brief test for "experimental extinction" from the 137th to 145th trials showed that it could be brought about by 7 presentations of the conditioning stimulus if this was not succeeded on each occasion by shock. One single reinforcement by a shock was adequate for its re-establishment.

A series of parallel experiments on this individual when daylight adapted was begun on January 20th (see later).

Specimen F. The discrimination of different intensities of neutral grey. (Recorded in full in Section III, Table II.)

Specimen G. The discrimination of monochromatic red from monochromatic yellow-green and pure green.

The conditioning stimulus was Wratten filter No. 70, transmitting 650–700mμ with a total transmission of 0·6%.

The discriminatory stimuli were filter No. 73 (Yellow-green), transmitting 560–620mμ, and No. 74 (Pure Green), transmitting 510–570mμ. Both of these had the same total transmission of 3·3%.

The conditioning stimulus acted for 3 seconds and the differential stimuli for 120 seconds.

The first conditioned reaction occurred at the 44th trial, and remained fairly stable to the conclusion of the experiment. The evidence for capacity to discriminate the differential stimuli from the positive conditioning stimulus was not so clear as in others, judged numerically. Up to the 87th trial no indication of discrimination could be obtained. Thereafter, whilst in some instances movement occurred to both green and yellow-green, the movement was very different in nature from that given to the positive stimulus of red, being slow and leisurely and contrasting sharply with the quick conditioned reactions. The experiment occupied from April 7th to May 6th, with a total of 126 trials.

Specimen H. The discrimination of magenta from grey, red, green, and blue.

The positive conditioning stimulus was magenta (filter No. 32).

The differential stimuli were as follows :—

Stage Red (No. 27).
Dark Toluidine Blue (No. 38A).
Green (Minus Red, No. 58), transmitting 490-590mμ ; total transmission 23%.
Neutral Grey (No. 96) of three different densities :—

Density 2·0. Total transmission 1·0%.
,, 1·5. ,, ,, 3·2%.
,, 0·6. ,, ,, 25·0%.

The positive conditioning stimulus preceded the stock by one second; the discriminatory stimuli acted for 120 seconds. The experiment began on January 12th and was completed on April 24th, after a total of 320 trials.

Conditioned motor response was first obtained at the 21st trial on the 6th day of actual experiment, but was not stable until after the 39th trial. From the 40th trial to the conclusion of the experiment, a well-marked positive response was given to the positive conditioning light (magenta) upon 126 out of 138 presentations. The occasions when no response occurred were confined solely to those tests which were the first of those made on several different days. Evidence of discrimination, irrespective of intensity variations, was obtained with all the differential colours (constantly presented without shock). This was most clear for neutral grey, with 100% negative responses (to all its densities and intensities) after the first three presentations. For the other colours the evidence is not satisfactory when examined as numerical totals, but is quite clear upon inspection of the daily behaviour. These colours usually evoked a positive response at their first trial of the day, but successive presentations upon the same day were followed by no response, whilst the primary positive stimulus presented next in sequence was found to yield a strong response. Such behaviour shows undoubted evidence of discrimination. The following extract from the log of a typical day's trials illustrates this point:—

[Explanatory notes as for Table II.]

1. Date. Times when put in and taken out of apparatus.	2. Time of each trial.	3. Number of trial.	4. Nature of signalling stimulus.	5. Resultant movement to 1. Signalling stimulus.	6. 2. Shock. S.=Shock. R.=Response.
April 2 [**20** 05; **21** 40]	**20** 20, **20** 25	251, 252	Magenta (No. 32)	Strong at once	Strong R
	20 30	*253*	*Red (No. 27)*	*Moderate at once, no further in 120″*	*No S.*
	20 35	*254*	"	*None in 120*	"
	20 40	*255*	"	" "	"
	20 45	256	Magenta (No. 32)	Strong at once	Strong R.
	20 50	*257*	*Grey (No. 96) 25% transmission*	*None in 120″*	*No. S.*
	20 55	*258*	*Blue (No. 38A)*	" "	"
	21 05	*259*	*Green (No. 58)*	" "	"
	21 10	260	Magenta (No. 32)	Strong at once	Strong R.

(b) Daylight-adapted fishes.

Specimen E. Continuing the investigation on Specimen E. The discrimination of green from red.

This individual was used for this experiment when it was already well "conditioned" to a visual stimulus under scotopic (dark-adapted) conditions. No essential departures from the method were made, except for the general conditions required for carrying out the tests in diffuse daylight. The positive conditioning stimulus was red (Stage Red, filter No. 27), preceding the shock by 3 seconds. The differential stimulus, green (No. 58), was allowed to act for 30 seconds. The experiment lasted from January 20th to February 10th.

No effect of the preceding scotopic treatment was apparent under the photopic conditions. The first conditioned response appeared at the 24th trial. Discrimination between the positive red and the negative green was clear.

After giving positive responses on each of the first two presentations of green, 24 negative responses were recorded in the remaining 28 trials with this colour. The notes already made relating to numerical treatment of these figures apply here also. Over the same period the primary positive conditioning stimulus of red, constantly reinforced by shock, gave 29 positive responses out of 33 trials. Total number of trials, 99.

Specimen J. Discrimination of magenta from grey, red, blue, green.

The experimental conditions for this specimen were identical with the last.

The positive conditioning stimulus was Magenta (filter No. 32). The differential stimuli (not followed by shock) were Grey (No. 96), Red (No. 27), Blue (No. 38A), and Green (No. 58).

The experiments were carried out over the same period as the experiments with Specimen H, and, as might be expected, with closely similar results.

Conditioned response first appeared at trial 51 on the 13th day of actual experiment, with, however, periods of several days when no experiments were possible. This response remained uniformly strong and characteristic to the conclusion at trial 168. Of the differential stimuli, grey again produced a clear-cut result, evoking no response at any time, not even at its first presentation. Blue also gave 100% negative responses, and green gave a positive reaction once only. Red was not clearly discriminated until the 100th trial of the series.

V. GENERAL SUMMARY AND CONCLUSIONS.

From the experiments described in this paper it is concluded that conditioned motor responses are readily formed in *Blennius pholis* L. by combining the presentation of a visual stimulus with an electric shock. This has already been found to be so in *B. gattorugine* and in certain other fishes. Further results will be given in Part V.

Evidence of discrimination for various wave-lengths of light may be deduced from the resultant behaviour observed in differential conditioning, in which one colour acts as a positive conditioning stimulus reinforced by electric-shock, and the colours discriminated are similarly presented but without succeeding shock. The discriminations inferred from the results are summarised in Table III. Those aspects of the results which concern, more particularly, theories of animal learning, will be considered together with other data in a later paper.

Some of the results of the wave-length discriminations are remarkable, particularly (1) the uniform evidence of the discrimination of grey from other colours whenever they have been contrasted; (2) the behaviour towards "white" light (Specimens A and B); (3) the absence of discrimination of varying intensities of grey. The results with grey considerably strengthen the conclusions which have been drawn upon the discriminations of colours.

The results with this fish appear to suggest that it has a definite and

TABLE III.

SUMMARY OF RESULTS RELATING TO WAVE-LENGTH DISCRIMINATION.

The numbers in brackets indicate the filter number.

Specimen.	Colour to which fish was positively conditioned.	Colours for which discrimination from the positive conditioning stimulus may be inferred from the results of differential conditioning.	Remarks.
1. *Scotopic* (*dark-adapted*).			
A.	Green (58).	Unfiltered "white" light from gas-filled electric lamp.	No differential conditioning required; discrimination shown from the start.
B.	Magenta (32).	,, ,, ,, ,,	,, ,, ,, ,,
C.	Magenta (32).	Red (27).	Discrimination after 3 trials.
D.	Red (27)	Magenta (32), Grey (96), Blue (38A).	See text.
	Orange-red (71).	Orange-yellow (72).	Discrimination after 5 trials.
E.	Blue (38A).	Magenta (32), Grey (96).	,, ,, 1 trial.
F.	Grey. (Threshold).	Lower intensities of Grey. down to 0·0018 × Threshold	NOT DISCRIMINATED.
		Grey, 0·00098 × Threshold—	Discriminated consistently.
G.	Red (70).	Yellow-green (73), Pure green (74).	See text; purely numerical evidence of discrimination not satisfactory.
H.	Magenta (32).	Grey (96), Red (27), Blue (38A), Green (58).	No differential conditioning required for grey, the others after varying amounts of differential conditioning.
2. *Photopic* (*daylight-adapted*).			
I.	Red (27).	Green (58).	Discrimination after 2 trials.
J.	Magenta (32).	Grey (96), Red (27), Blue (38A), Green (58).	No differential conditioning required for grey or blue; red and green discriminated after varying intervals.

wide range of colour vision as we ordinarily speak of it, although there is no reason to suppose that we can extend this conclusion to other fishes. These experiments emphasise the difficulty of getting reliable objective evidence upon wave-length discrimination in fishes. The method is only applicable to sedentary fishes. A comparative survey of the state of knowledge upon " colour vision " in fishes which had been prepared for inclusion in this discussion has been made unnecessary by the appearance of L. H. Warner's admirable summary (**3**) to which reference should be made. A complete index and bibliography of the literature on the experimental study of " colour vision " in fishes is to be found in (**4**) compiled by the present writer in collaboration with Dr. E. S. Russell.

My thanks are due to Professor A. D. Hobson for his helpful criticism, and especially to Dr. E. J. Allen for his never-failing help and encouragement.

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Studies on Conditioned Responses in Fishes. Part V. On the Controlling Influence of Normal Behaviour Traits upon Capacity to Form Experimental Conditioned Motor Responses Under Certain Conditions.*

By

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In Part III of these studies (**3**) it was shown that *Blennius pholis* readily forms conditioned motor responses towards lights of various wave-lengths when these are associated with a succeeding electric shock. Many experiments were required to establish an adequate knowledge of the capacity of this species of fish to discriminate between these various wave-lengths. It was possible, however, that all species of fish would not be equally suitable for this type of experiment. In view of this some preliminary experiments were made with other species. A condensed account of some of these results is given in this paper chiefly because they reveal a striking difference between fishes belonging to the Pleuronectidæ and those belonging to the other families investigated. Fishes belonging to the Pleuronectidæ were found to be incapable of forming conditioned motor responses to a circle of light when this was associated with a succeeding electric shock. The other fishes investigated readily formed such conditioned responses.

The experiments were carried out at night in the special sound-insulated building described in Part IV (**4**). The procedure was that of the earlier experiments described in Part III (**3**). Only those fishes were used which were in a thoroughly healthy condition and behaved in captivity in the manner typical of their kind. They were normally kept in specially reserved tanks in the aquarium under personal supervision. Each day of trials the fish was transferred to the experimental apparatus (described in Parts I and III, **1**, **3**) approximately 30 minutes before the first conditioning test; it was then given an average of 8 conditioning tests; after a further period of rest of approximately 30 minutes it was returned to the tank where it normally lived.

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* Part IV has appeared in the Report of the Dove Marine Laboratory, Cullercoats, year ending 1st July, 1934. It is devoted solely to the description of a sound-insulated building erected for the purpose of carrying out these researches under more constant conditions and free from extraneous influences.

The conditioning test was the same for all. A circle of light 1·5 inches in diameter, at a distance of 5 inches from the fish was formed by the light from a 100-watt lamp transmitted through a Wratten light filter No. 32 (magenta). Full particulars of the arrangement and the method of noting the response of the fish are given in the earlier paper (Part III, p. 348 *et seq.*). An electric shock was given to the fish at the same instant as the making of the same circuit produced the circle of light. By giving the electric shock simultaneously with the light in this way it follows that, even if the fish were becoming " conditioned " any conditioned motor reaction would be masked by the supervening shock reaction. Hence for the purpose of ascertaining the progress of " conditioning " the light was shown periodically without the associated shock. This may be seen in the log of the experiment on *Spinachia vulgaris* in Table I.

This simultaneous " conditioning " was attempted for a special reason which will be discussed fully at a later date, but is here briefly outlined. There are, as is well known, two essentially opposed groups of theories of animal behaviour : (A) Mechanistic, reflex, tropistic, etc. (B) Vitalistic, hormic, conative or " goal-seeking," etc. Leading exponents of (B) say unequivocally that we should *accept as granted* an inherent conative or goal-seeking tendency in animal behaviour (**5**). Of various avenues of approach, the study of animal learning has provided a large part of the material from which the conception of conative activity is derived. An integral part of this conception is the expression of *laws* of learning in terms of an animal's *needs* and the *satisfaction* of those needs. Critically and competently used such a concept and such expressions may be valuable as an aid in the description or the comprehending of facts, or sequences of events in animal reaction, whose real nature is for the time elusive. Objective enquiry can hardly rest content with this facile type of descriptive interpretation. If, for example, it could be shown in a sufficient number of representative animals that truly simultaneous conditioned reflexes (in the strict sense) or responses (in the broader sense) could be established, and that they followed the same course as general learning activity where conation is accepted by school B it would be possible to say that the two processes had a common basis and that it was highly probable that the latter (being the more complex) could be derived directly from the former. This would mean that conation had a basis which one might fairly expect to elucidate analytically, for it is clear that a strictly simultaneous conditioned reflex cannot have a conative basis.

The present experiments make no attempt to offer conclusive evidence upon this point. They do show, however, that in those fishes where conditioning has been established it *is* possible to use simultaneous presentation of the unconditioned with the conditioning stimulus, but that the conditioned response itself, as noted by the registration of total

TABLE I.

RECORD OF AN EXPERIMENT ON *Spinachia vulgaris* (L) SHOWING THE FORMATION OF A CONDITIONED MOTOR RESPONSE TOWARDS THE VISUAL STIMULUS OF A CIRCLE OF MAGENTA LIGHT, USING AN ELECTRIC SHOCK AS THE UNCONDITIONED STIMULUS. LENGTH OF SPECIMEN 13·5 CM.

Date, times, etc.	Time of Expt.	Serial No. of Expt.	Resultant movement to	
			A. Signalling Stimulus.	B. Electric Shock.
Feb. 23 [put in app. 17 00 ; removed at 18 50]*	17 50, 55 ; 18 00, 05, 10, 20	1 to 6		Strong.
	18 25	7	None	No S.†
	18 30	8		Strong.
Feb. 24 [put in app. 17 10 ; removed at 19 10]	18 15, 20, 25, 30, 35, 40	9 to 14	—	,,
	18 43	15	None	No S.
	18 45	16		Strong.
Feb. 26 [put in app. 17 30 ; removed at 18 25]	17 50	17	—	,,
	17 55	18	V. slight at 4 sec.	No S.
	18 00, 05, 10	19 to 21	—	Strong.
Feb. 27 [put in app. 19 00 ; removed at 20 20]	19 30, 35	22, 23	—	,,
	19 40	24	Moderate at 3 sec.	No S.
	19 45, 50	25, 26		Strong.
	19 55	27	None	No S.
	20 00	28	—	Strong.
March 1 [put in app. 18 25 ; removed at 19 35]	18 45	29	—	,,
	18 50	30	Vigorous at 1 sec.	No S.
	18 55	31	—	Strong.
	18 58	32	Distinct at 2 sec.	No S.
	19 00	33	—	Strong.
	19 05	34	Vigorous at 0·4 sec.	No S.
	19 10	35	—	Strong.
	19 12	36	Vigorous at 1 sec,	No S.
	19 15	37	—	Strong.
March 3 [put in app. 21 02 ; removed at 22 10]	21 30, 35	38, 39	—	,,
	21 40	40	Distinct at 2·4 sec.	No S.
	21 45	41		Strong.
	21 47	42	Strong at 1·2 sec.	No S.
	21 50	43	Strong at 0·8 sec.	,,
	21 55	44	—	Strong.
March 5 [put in app. 18.15 ; removed at 19 20]	18 30	45	—	,,
	18 35	46	Strong at 2·8 sec.	No S.
	18 40	47	—	Strong.
	18 45	48	Strong at 3·0 sec.	No S.
	18 50	49	Distinct at 2·4 sec.	,,
	18 55	50	—	Strong.
	18 58	51	Strong at 1·2 sec.	No S.
	19 02	52	,, 0·4 sec.	,,
	19 04	53	,, 0·2 sec.	,,
	19 06	54	,, 0·2 sec.	,,
March 6 [put in app. 20 10 ; removed at 21 15]	20 30	55	—	Strong.
	20 35	56	,, 0·6 sec.	No S.
	20 40	57	,, 0·8 sec.	,,
	20 45	58	—	Strong.
	20 50, 55	59, 60	,, 0·2 sec.	No S.
	21 00	61	—	Strong.
March 7 [put in app. 21 10 ; removed at 22 30]	21 40	62	—	,,
	21 45	63	,, 0·2 sec.	No S.
	21 50	64	—	Strong.
	21 55	65	,, 0·2 sec.	No S.
	22 00	66	,, 1·4 sec.	,,
	22 05	67	,, 1·2 sec.	,,
	22 10	68	,, 2·6 sec.	,,

* Times when fish was put in apparatus and removed.
† No S. signifies no electric shock given (see text p. 366).

body movement, is delayed by a short period varying from a fraction of a second to 2–3 seconds. At least 0·2 second of this is definitely due to time-lag in the recording mechanism, and it would seem that in those instances where the recorded response takes place at 0·2 second after the application of the conditioning stimulus that the result approximates closely to the demands of the above postulate. More elaborate technique is necessary to give a satisfactory answer to this aspect of the experiments.

It has not been thought necessary to give the full details of the experiments, but one typical log is given as an example (Table I, *Spinachia vulgaris* (L)). This shows the salient features of all the experiments, the remainder of which are summarised in the succeeding table (Table II).

TABLE II.

Summary of Present Series of Experiments on Several Teleostean Fishes showing the Variation in their Ability to Associate the Visual Stimulus of a Circle of Magenta Light with an Electric Shock.

Species.	No. of associations before 1st appearance of the conditioned response.	Percentage of positive responses to light alone after the 1st appearance of the c.r.	Latent period of response. General statement. Seconds.	Total number of associations in experiment.
1. *Cottus bubalis* Euphrasen .	37	100	0·5–3	93
2. *Spinachia vulgaris* Flem. .	18	96	0·2–3	69
3. *Onos mustela* (L.) . .	17	100	0·4–4	52
4. *Liparis montagui* (Donovan)	16	92	0·2–4	64
5. *Zoarces viviparus* L. . .	34	92	0·8–4	87
6. *Centronotus gunnellus* (L.) .	36	77*	0·6–4	90
7. *Rhombus maximus* L. . .	Not formed	—	—	233
8. *Pleuronectes platessa* L. .	,,	—	—	203
9. *Pleuronectes flesus* L. . .	,,	—	—	203

It is to be seen that the three Pleuronectid fishes have reacted in a manner markedly different from the remainder, and that they have been found incapable of forming a conditioned response under these conditions for at least 200 associated presentations, whilst the other fishes have done so in less than 40 such presentations. In addition it has already been extensively shown (Part III) that *Blennius pholis* readily forms this response in a comparatively short number of trials; so, too, with *B.*

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* 100% after the 66th association.

gattorugine (Part I, pp. 527 *et seq.*). Further, consistently negative results for over 200 trials were obtained in an earlier (unpublished) experiment with a small turbot (*Rhombus maximus*) where light was similarly used as a conditioning stimulus in association with a sharp tap with a pointed glass rod.

On the other hand, in contrast with these results with a harmful unconditioned stimulus, it has been shown that where a visual conditioning stimulus is used in association with a harmless one such as a *food*, no real difficulty is experienced in establishing associative behaviour in Pleuronectids (Part II, p. 620). At the same time attention has already been drawn to a distinctive feature in the behaviour of Pleuronectids in that type of experiment which appears to harmonise with the present observations (Part II, p. 621).

It is here that the study of the organism in the field recently emphasised by E. S. Russell (**5**) helps to throw light. Pleuronectids in general are peculiarly well adapted to escape from enemies by a mechanism of concealment comprising (*a*) adaptation to colour of background; (*b*) "freezing" or keeping still (so far as is practicable) when alarmed. This behaviour is well known to all who have pushed a shrimp net along a sandy shore after flat-fishes.

The other fishes used in these experiments all exhibit, with or without modification, a well-marked "flight" reaction when alarmed. It is concluded, therefore, that the *normal* reaction of these respective types of fish to a harmful or threatening stimulus exercises a controlling influence over the *experimental* formation of conditioned motor responses when these are investigated on the basis of a similar stimulus (i.e. an electric shock). In looking for an explanation of the nervous mechanisms involved in conditioned behaviour this correlation provides something definite upon which to build.

It also follows that Pleuronectid fishes are unsuitable for the investigation of visual discrimination by conditioning on those lines, but that no difficulty should be experienced with the other fishes mentioned.

My thanks are due to Professor A. D. Hobson, M.A., for his criticism and advice.

SUMMARY.

Normal behaviour traits control the ability of fishes to form conditioned motor responses. This is shown by a series of experiments upon various species of fish in which it is found that Pleuronectids are found incapable of forming such responses for at least 200 associated presentations whilst other fishes have done so in less than 40. The bearing of the results on current theories of animal learning is briefly discussed.

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Hemiurus communis in Acartia.

By

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In tow-nettings from Plymouth Sound, June 20th, 1935, *Acartia clausi* were abundant and inside these copepods, emerging from them and free in the water were very large numbers of larval trematodes, easily identified as *Hemiurus communis*. This is not a new record, for this parasite has already been described from the same Copepod in Plymouth waters in May and February (Lebour, 1923), but it has always been rare. In no case have more than two parasitised specimens been seen from these regions, and no seasonal appearance has been noticed. Much has been written about these trematodes which grow in the bodies of copepods until they are of such a large size that they inevitably kill the host and just before it dies emerge from between the joints, if not eaten before this with the copepod, but I think this is the first time that they have been recorded in any quantity at one time. Since my first communication Steuer (1928) has written about the geographical distribution of these hemiurids parasitising copepods and is of the opinion that all those in Northern seas belong to *Hemiurus lühei* and *H. communis*. In the Mediterranean the hemiurids known have not yet been found in copepods but usually in Sagitta, or are found living freely in the sea and these probably belong to *H. rugosus* which lives in the adult state in the pilchard.

Dollfus (1923) summarises the records of trematodes found in copepods, including my own from *Acartia clausi* and agrees with the identification. He discusses the life-cycle of this trematode and of the two hypotheses put forward by workers, that the miracidium emerging from the egg penetrates directly into the copepod, or that another host is required, inclines to the second. He believes that the miracidium enters some mollusc, the cercaria resulting from the redia or sporocyst then penetrating the copepod which in this case would be the intermediate host. In support of this theory he suggests that a curious cercaria, named by him *Cercaria calliostomæ* and found frequently in rediæ in the marine gastropod *Calliostoma conuloides*, belongs to a species of *Hemiurus*. This has a very peculiar form, having a cyst at the hind end of its body and a long tail. This cercaria belongs to the group of *Cercaria cystophora* Way, living both in fresh and salt water and occurring both in fresh-water and marine gastropods, tectibranchs, pteropods and pectinibranchs. *Cercaria cystophora* is the larva of a *Halipegus*, a genus belonging to the super-family Hemiurida. There is certainly something in this suggestion.

The occurrence of these worms in quantity as recorded above suggests the emergence of a swarm, or swarms, of cercariæ which might well have come from some bottom mollusc in the Sound, which have risen to the surface waters on emergence from this host and have entered into the numerous Acartias swimming there. In the copepods they would grow, feeding on their body fluid until of so large a size that it was impossible to grow any more inside the host and it would then be time to emerge. Many of these trematodes had the intestine full of a bright pink fluid, probably a result of feeding.

One curious thing seen in the plankton sample was a larva (trocophore) of the worm Polygordius to the outside of which were attached two of these trematodes. These were firmly fixed by their oral suckers, and when kept overnight were still alive and had not let go their hold.

Hemiurus communis is one of the commonest fish trematodes, occurring in many species but especially in gadoids, the young of which feed almost exclusively on copepods. In working on the food of young fishes I found *Acartia clausi* in post-larval *Gadus merlangus* (the whiting) besides several other species. It is probable that very young fishes eat the copepods and quite small specimens are found parasitised by trematodes. In examining six small whiting (25 to 40 mm. long), three were found to contain trematodes. These were *Derogenes varicus*, a form not distantly related to Hemiurus.

It is probable that many trematode parasites enter their hosts when the latter are very young.

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The Breeding of *Littorina neritoides*.

By

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With 11 Figures in the Text.

Littorina (*Melarhaphe*) *neritoides* (Montagu) is stated by Tattersall to be viviparous. Living usually above high-water mark, often with *Littorina saxatilis* (*L. rudis* in Plymouth Marine Fauna 1931, Marine Biological Association), it would seem at first sight that free-swimming larvæ would be useless. *L. saxatilis* is truly viviparous and provided with a special pouch for its young which crawl out as small individuals similar to the parent. Tattersall (1908, 1909, 1920) when he discovered the planktonic egg-capsules of *L. littorea* (Caullery and Pelseneer (1910) having described them at almost exactly the same time) then regarded *L. neritoides* as viviparous. He has, however, kindly sent me the statement given below.* Following him many workers have also declared that this species is viviparous (Flatteley and Walton, 1922, Colman 1933 Russell, 1934 and others). It is now possible to show that, not only is it not viviparous but it lays planktonic capsules very similar to those of *L. littorea*.

It was with surprise that I could never find any young inside *L. neritoides* although they were always to be found in *L. saxatilis*. Moreover, although their usual habitat is in crevices of dry rock where only spray on rare occasions can reach them (Figs. 10 and 11),† I also found them at times in small shallow pools a few inches deep in the rocks. At Wembury, below the cliffs and sometimes covered at high tides, they are to be found with *Monodonta lineata* (*Osilinus lineatus* of the Plymouth Fauna, 1931) which sends its eggs out singly into the water in a similar way to Gibbula. Robert (1902) states that it is probable that Monodonta should do this and I have found in this species ripe eggs which are surrounded by a gelatinous layer swelling up in the water in exactly the same way as in Gibbula. On the other hand Colman (*op. cit.*) states that *L. neritoides* at

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* The statement in my paper on the breeding of *Littorina littorea*, that *L. neritoides* is viviparous was based on similar statements which I thought I had read in the literature of the subject. I cannot now trace the source of this information. I have never observed viviparity in this species myself nor indeed investigated the problem at all.

† Mr. D. P. Wilson has kindly supplied me with two photographs of *L. neritoides* in their natural habitat.

Wembury "extend up the rocks several feet above high-water mark where for weeks during a calm summer their sole source of moisture is dew, rain, if any, and perhaps the dampness caused by the salt on the rocks. They congregate not only in cracks and crannies where it is damp, but also in hollows which are quite dry and bare and also directly facing the sun. It is possible that this search for hollows and cracks is more an avoidance of the mechanical force of the wind than of the dessication caused by it." Below the Plymouth Laboratory they are to be found in numbers high up in the cliffs, but sometimes in small pools in the crannies.

I studied this species for many months to see if it laid eggs, but was unsuccessful. At the same time I was finding the eggs and young of many shore prosobranchs, amongst them *Rissoa sarsii* whose larvæ are so common in the plankton in winter and serve as food for the very young herring (Lebour, 1933, 1934). I then attributed to *R. sarsii* a planktonic egg capsule, somewhat similar to that of *Littorina littorea* but much smaller, of a different form, and containing only one egg. I never succeeded in obtaining this capsule from the Rissoa itself but the identification was in accord with the fact that the shell of the veliger inside the capsule was sculptured in the same way as those very young larvæ from the plankton eaten by the herring and certainly belonging to *Rissoa sarsii* (later larvæ of the same species having been reared to the adult stage), the planktonic capsules occurring at the same time. This identification of the planktonic capsule is now found to be erroneous for the *Rissoa sarsii* reared from the late larvæ which were certainly the same species as the young eaten by the herring, laid eggs in the aquarium and there were in typical sessile rissoid capsules, lens-shaped, containing several eggs and attached by the flattened base to weeds. All known rissoids therefore have a similar type of egg capsule and the planktonic capsule must belong to some other mollusc.

At the same time that I was making these observations Dr. Otto Linke of Leipzig was carrying on researches on the reproductive organs of the Littorinidæ (1933). During a correspondence in which I suggested that *L. neritoides* was not viviparous he agreed, indeed he said he was sure it was not, and, later, he told me that he thought he had obtained pelagic egg capsules from it, somewhat similar to those of *L. littorea*. His sketch of the capsule was very similar to the capsule which I had attributed to *Rissoa sarsii*. This observation made me redouble my efforts to obtain eggs from *L. neritoides* and quite recently I found inside some of them eggs surrounded by true capsules, which, although much softer than those in the plankton, were of the same form and size. On writing to Dr. Linke on this matter he told me that he had recently obtained the capsules actually laid by the mollusc. He kindly allows me to refer to his discoveries and he is certainly the first to find that *Littorina neritoides* undoubtedly lays planktonic egg capsules. His specimens came from Rovigno and breed in late winter and spring. In Plymouth the capsules are found in the inshore plankton through the winter and early spring, and they were found inside the female, ready to be laid, in April.

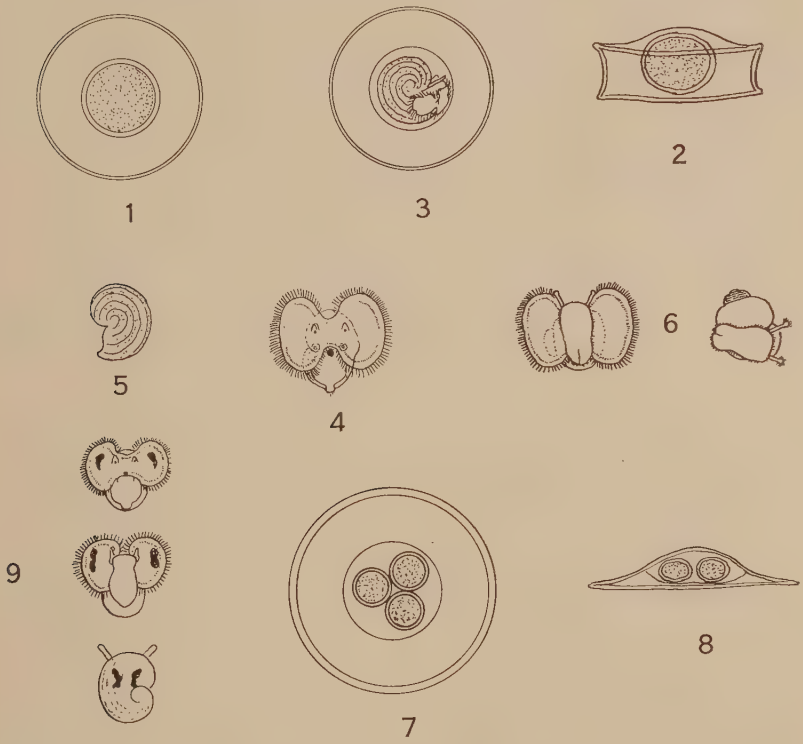


Fig. 1, 2.—Egg capsule of *Littorina neritoides* from plankton, newly laid, 0·18 mm. across.

Fig. 3.—Egg capsule from plankton with veliger nearly ready to hatch.

Fig. 4.—Veliger from plankton, presumably belonging to *L. neritoides*, shell 0·06 mm. across.

Fig. 5.—Shell of same.

Fig. 6.—Late veliger of *Littorina* sp., possibly *L. neritoides*, shell 0·54 mm. high.

Fig. 7, 8.—Egg capsule of *Littorina littorea* 0·96 mm. across.

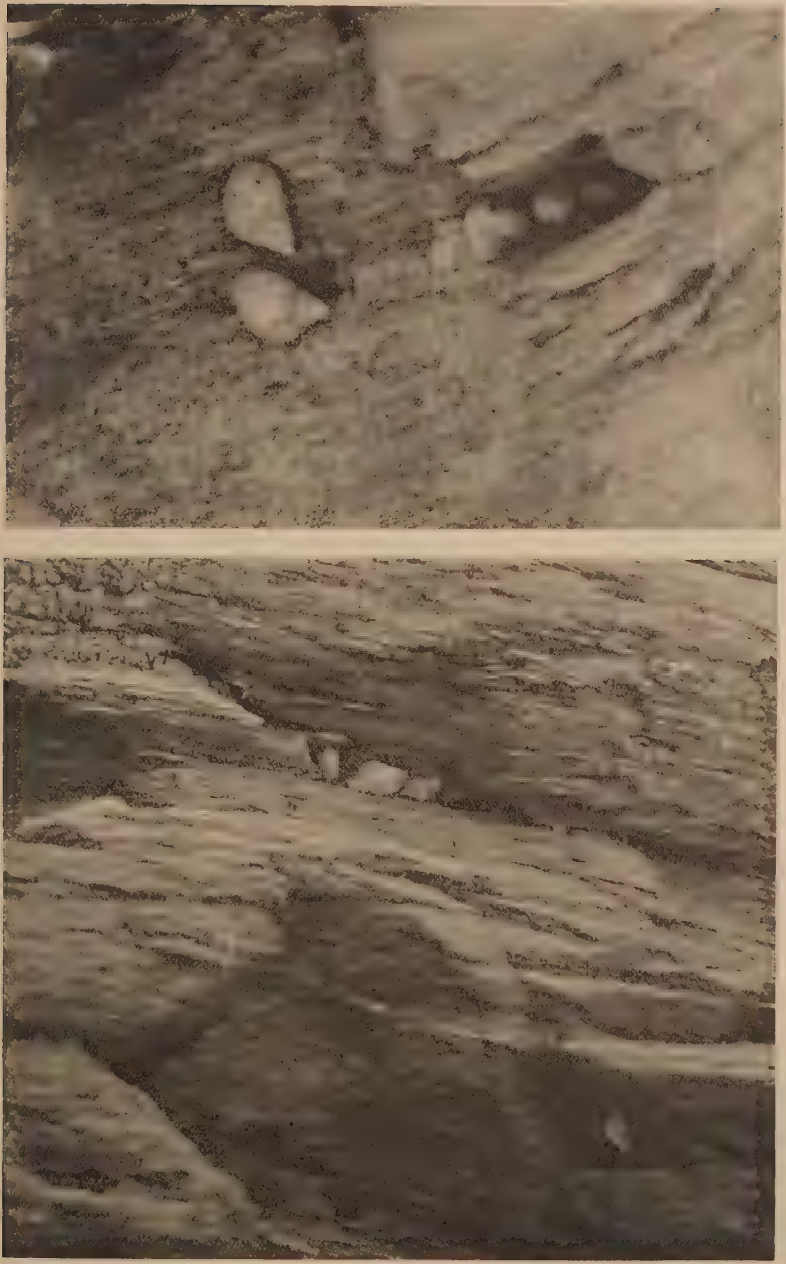
Fig. 9.—Veligers of *L. littorea*, swimming and crawling, shell 0·48 mm. to 0·5 mm. across.

This exceedingly interesting find shows that the capsules must somehow get into the water and the fact that the molluscs have been found in shallow pools in the rock crannies probably shows their method of reaching the sea. It may be that those very high up in the dry rock crevices move towards water in the breeding season. It is certain that the capsules occur fairly commonly in the coastal plankton in winter and spring. It is more difficult to conceive how the crawling young reach the dry rocks. Possibly the spray deposits them near, or very high tides.

A figure of the capsule is repeated here (Figs. 1–3) together with one of *L. littorea* for comparison (Figs. 7–8). The capsule of *L. neritoides* measures 0·16 to 0·18 mm. across, 0·09 mm. high, the newly laid egg 0·08 mm. across. The capsule of *L. littorea* measures 0·96 mm. across.

The egg is covered by a thin membrane and bathed in a fluid surrounded by an egg covering (=egg capsule of Linke). Surrounding this is the capsule (=laich of Linke) which is circular in outline, rounded in the centre on both surfaces, one surface more rounded than the other (Fig. 2). Eggs in all stages can be found in the plankton, finally a shelled veliger is seen, the velum with long cilia, the shell being sculptured with spiral lines and dots in between in a similar way to that of *Rissoa sarsii*. Early free-swimming veligers in the plankton have probably been mistaken for those of *R. sarsii* being, however, rather smaller when newly hatched (Fig. 3). There is sometimes found in the coastal plankton round Plymouth a late veliger (Fig. 6) which is apparently a species of Littorina and which does not belong to *L. littorea*, the latter species being recognisable by the two distinct dark purple marks one on each side of the velar lobes. Also *L. littorea* metamorphoses at a smaller size (Fig. 9). This unknown veliger has a perfectly colourless velum and a dark brown shell of about 2½ whorls with faint striation. In shape the shell is much like a late rissoid larva, metamorphosing at much the same size and with 2½ whorls being able either to swim or crawl. The animal, however, shows it to be a Littorina. It occurs in spring and summer coastal plankton and may possibly belong to *L. neritoides*. If this be a correct identification then the fact that it remains long in the plankton and metamorphoses at a comparatively large size may account for its being able to migrate to some extent in order to reach the dry rocks.

All this emphasises the fact that it is not a fixed rule for those molluscs inhabiting regions beyond or near high water mark to be viviparous or have the veliger stage suppressed.



Figs. 10 and 11.—*Littorina neritoides* in its natural habitat in the rock crevices (photographs by Mr. D. P. Wilson).

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Copepods from the Interstitial Fauna of a Sandy Beach.

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With 10 Figures in the Text.

Attention was first drawn by Wilson (1932) to the large copepod fauna which can be found in an ordinary sandy beach. In his introduction he describes his method of collecting these copepods (p. 7) and in the course of the paper describes a number of new genera and species thus obtained.

Sand-dwelling animals, particularly crustacea and worms (excluding sessile forms), are usually regarded as burrowers, since in their migrations they displace the particles of their environment. The fauna opened up by Wilson's discovery is of a quite different type. In contrast to true sand-burrowing animals, these copepods do not displace the particles of the sand through which they move but crawl over the surface of the grains, which, by capillarity, always hold more or less water, even high up on the beach at low tide. Such copepods, together with nematodes, rotifers, protozoa and other animals sufficiently small, may be regarded as part of an " interstitial " fauna.

As pointed out by Wilson they are feeble swimmers and move with a wriggling motion resembling that of a worm. The wriggling motion, moreover, is incessant so that it is almost impossible to distinguish species while alive and, of course, quite impossible to obtain even approximate measurements of length. They become quiescent only when in a moribund condition or when crawling over sand grains when, owing to their transparency, they are almost invisible.

Copepods of this type, though members of different families, have a number of features in common. They are all elongate and cylindrical, with practically no demarcation between the metasome and urosome, and many bear, on one or more pairs of the swimming legs, modified setæ of a peculiar type (hastate setæ) not found in copepods from other habitats. This type of seta is common to two copepods which, from other considerations, must belong respectively to the Ectinosomidæ and Canthocamptidæ which suggests that this development is an environmental adaptation rather than an indication of morphological affinity.

The different species, moreover, show an almost specific distribution from low water to the highest part of the beach, which is submerged only by the highest tides and may receive large quantities of fresh water in the form of rain both directly and by drainage. The copepods of the interstitial fauna show, in some cases, specific vertical distribution, some species being restricted to the top two or three centimetres of sand while others may be found only below 3 cm., at least during the period of tidal exposure. Thus those species which inhabit the higher parts of the beach and are superficial may be subject to considerable changes in salinity. The ability to withstand such changes is probably the major factor controlling the distribution of species.

I have to thank Mr. R. Elmhirst for the series of sand samples from which this information on the horizontal distribution of species was obtained. It was from these samples that the discovery was made of the presence of copepods high up the beach and also of several of the new species herein recorded.

The beach in question is Kames Bay, Millport, an area of some 11 acres, bounded at the highest part by a concrete promenade and sea-wall, and at both ends by rocks. The linear extent of tidal range is about 150 yards and only occasionally does the sea reach the promenade.

Several of the copepods found in the Bay are new species referable to genera erected by Wilson. The others have to be placed in new genera. All appear to breed continuously though they are undoubtedly more numerous during the spring and summer than later in the year. The method of collecting did not differ materially from that described by Wilson.

Formalin-preserved material has been used throughout and lengths are given in millimetres. All measurements of total length are from the tip of the rostrum to the end of the caudal rami and do not include the caudal setæ. Measurements can, of course, have little or no specific value since they were, of necessity, on preserved material and a certain amount of alteration occurs on preservation, quite apart from the general unreliability of measurements of such animals as copepods, whose body segments are telescopic. The lengths are given because they give some idea of the relative difference between male and female or between species, such a difference being one which strikes the eye and helps in identification. They are given to two places of decimals because without the second place the majority would appear to have the same length. The scale shown with each figure applies only to the whole animal. The appendages, except where otherwise stated, are drawn to a scale equal to 1·8 times that shown. The drawings have all been made with the aid of a *camera lucida*.

Family **ECTINOSOMIDÆ.**

Wilson has already recorded one new genus, Arenosetella, from a similar habitat and belonging to this family. One of the copepods occurring here, while undoubtedly an Ectinosomid, does not belong to any of the known genera. In shape it most closely resembles Arenosetella, in which feature both depart from the fusiform shape typical of the family.

Genus HASTIGERELLA gen. n.

Body cylindrical, slender, without definite demarcation between metasome and urosome, but tapering somewhat posteriorly. Urosome 4-segmented in female, 5-segmented in male. Head fused with first segment; rostrum prominent and well defined at the base. Antennule 6-segmented in female, 7-segmented in male. Antenna with 2-segmented exopod attached to the distal end of the first segment of the 3-segmented endopod. Upper lip bearing a median palp. Mandibular palp well developed, with small 1-segmented exopod. Maxilla armed with two long powerful claws and three more slender setæ terminally; basal endites represented only by setæ. Maxilliped reduced. Both rami of legs one to four with three segments, the exopod in each case bearing one or more hastate setæ. Segments of the fifth legs almost entirely fused. Caudal rami short and tapering, each bearing one long apical seta. The choice of generic name was decided by the extensive development of the hastate setæ in this animal.

Remarks. In its general shape and in its habitat this genus resembles Arenosetella, but the two segments of the fifth legs are fused and the claws on the anal segment are lacking. As in Pseudobradya there are only two segments in the exopod of the antenna. The mandibles and maxillules are similar to those of Microsetella and the maxillæ and maxillipeds resemble those shown by T. and A. Scott (1896) for various Ectinosoma species but are more reduced than any figured by them. Thus it has many points in common with the several genera of the Ectinosomidæ but cannot be included in any one. The acute point on the upper lip in Ectinosoma appears in Hastigerella as a palp or filament, distinctly separated at the base and tipped with setæ.

Hastigerella palpilabra sp. n. (Figure 1).

Female. Body segments about equal in size except the anal segment which is about half the preceding one. Segments of the posterior region of the body, except the anal and pre-anal, fringed behind with fine denticles. Caudal rami short truncated cones with one long terminal seta as long as the urosome, a second about half as long and two short

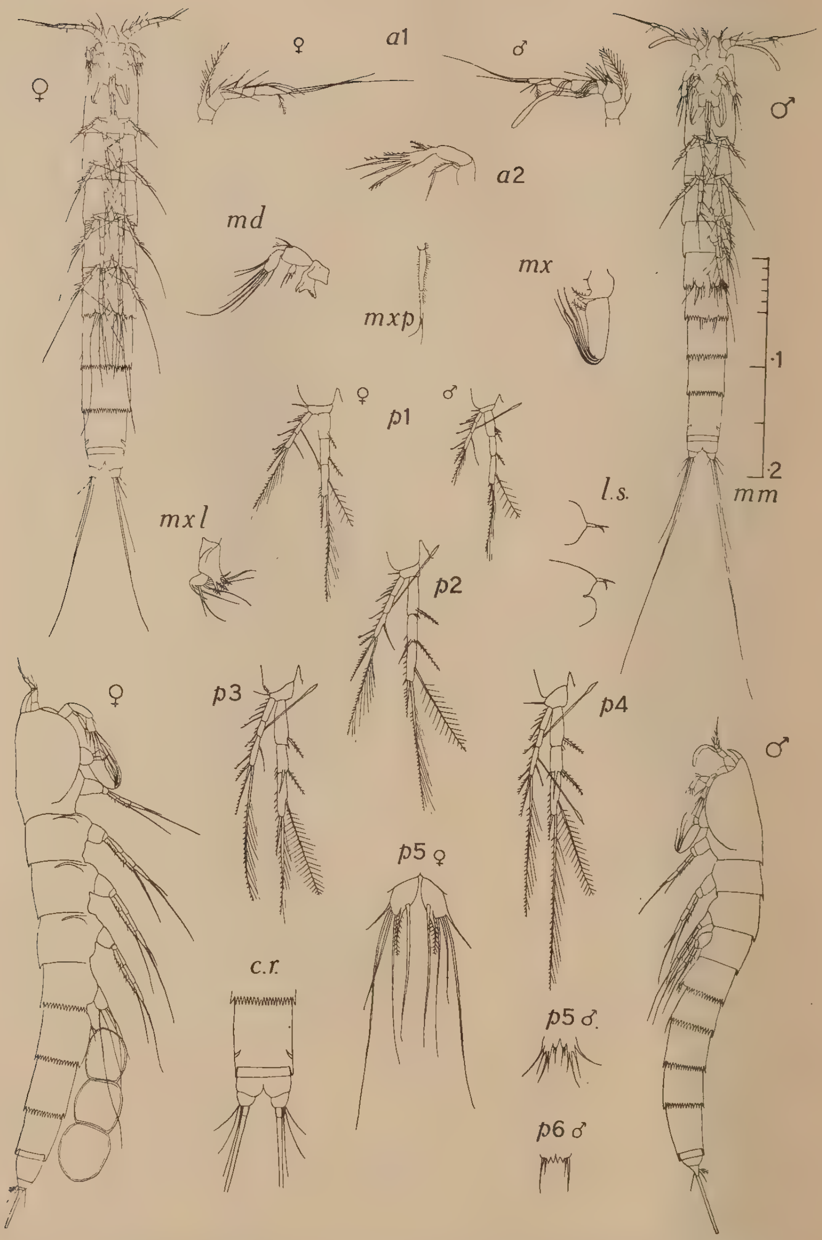
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Fig. 1.—*Hastigerella palpilabra* gen. n., sp. n. *a*1, antennule ; *a*2, antenna ; *l.s.*, upper lip ; *md*, mandible ; *mxl*, maxillule ; *mx*, maxilla ; *mxp*, maxilliped ; *p*1–6, legs 1–6 ; *c.r.*, caudal rami and posterior region of urosome. The caudal rami are those of the female.

ones externally. None of these is armed. Rostrum large, curved and pointed, well defined at the base. Antennule 6-segmented, bearing one large plumose seta on the swollen inner side of the second segment; terminal segment with a small lateral plumose seta and two long terminal setæ, the longer equalling the length of the appendage. Antenna 3-segmented with a small 2-segmented exopod on the inner distal margin of the basal segment; exopod with one long and one short terminal seta and a row of fine hairs on the terminal segment. Upper lip with 1-segmented median palp tipped with two short setæ. Mandible with palp well developed; basal segment bearing two setæ, terminal segment with two marginal setæ, four long terminal setæ and one short seta; exopod consisting of one small segment with four terminal setæ. Maxillule with at least four short curved spines and a lobe bearing numerous long setæ. Maxilla 2-segmented; basal segment with endites reduced, represented by one short spinous seta and two small hairs; terminal segment with short spinous seta and small hairs basally, and tipped with two long curved denticulate spines and three slender curved setæ. Maxilliped a simple 3-segmented, linear appendage tipped with two short setæ, and fringed with fine hairs laterally. Both rami of legs one to four have three segments; the outer margins of the exopods have three to five spines on each segment and one long seta and two short spines terminally, the long seta being armed with spinules externally and with fine hairs internally. The second segment of the exopod in legs one to four bears one long hastate seta on its inner margin; the third segment has one short seta with an additional hastate seta in the fourth leg. The basal segment of the endopod bears one short spine distally, in legs one to four, on the inner margin; the second segment bears one in the first leg and two in legs two to four, distally; the third segment has a longer seta, coarsely plumose, on the inner margin with one long and one short seta terminally. The terminal setæ of both rami increase in length from first to fourth legs. The fifth legs show almost complete fusion of the two segments and are elongate and lamellar. There is a short seta outside, followed by one very long one, extending nearly to the end of the pre-anal segment, then two shorter setæ, one short plumose seta and a longer seta internally. The genital segment bears a pair of short setæ, one on either side of the genital aperture. A single egg-sac is carried containing usually three eggs, one behind the other. Length about 0·41 mm.

Male. Body similar to that of the female except that there are five segments in the urosome and the anal segment is about one-third of the length of the pre-anal. Caudal rami as in the female but the long setæ are about three-fifths of the length of the body; the other setæ are like those of the female with an additional small seta inside. Antennule

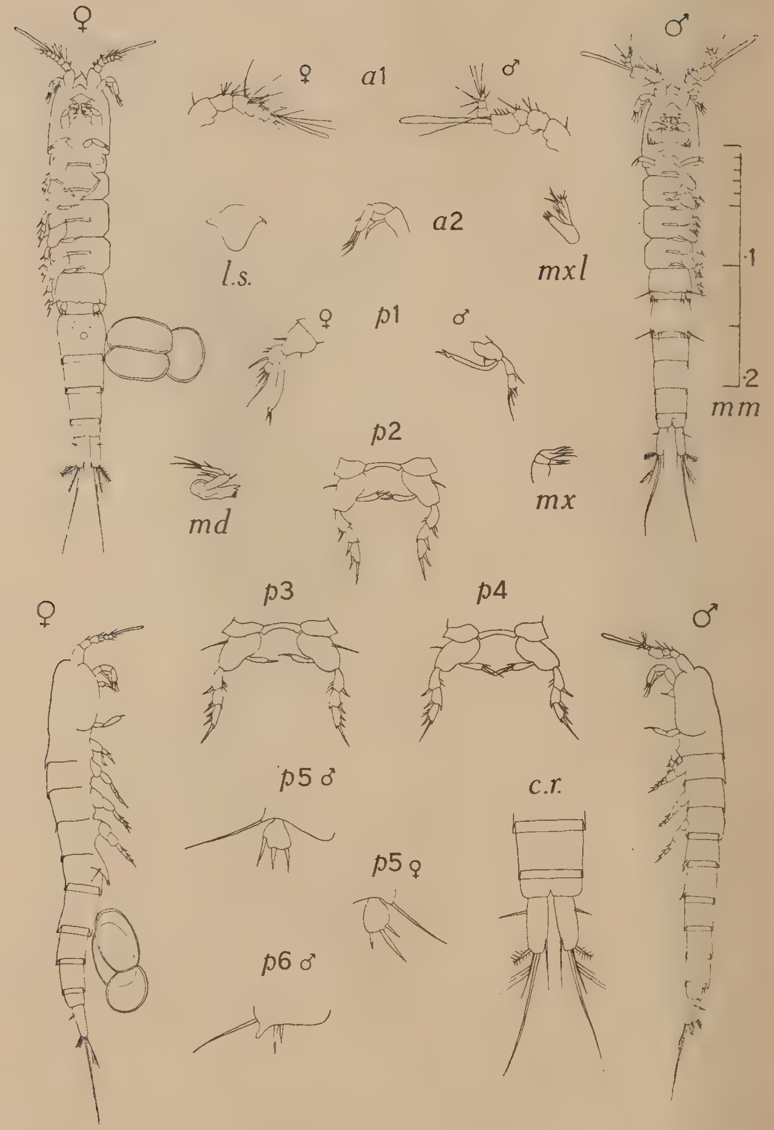
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FIG. 2.—*Leptopsyllus constrictus* sp. n. Lettering as in Figure 1. Fifth and sixth legs drawn to a scale 2·3 times that of the other appendages.

7-segmented, distinctly geniculate between the third and fourth ; a long plumose seta occurs on the second segment and a long curved æsthetasc is borne on the end of the fourth segment and extends beyond the end of the appendage ; a bunch of setæ occurs at the end of both fourth and fifth segments, otherwise the setæ are much as in the female. The mouth parts and legs are like those of the female but the legs are much shorter and the setæ not so strikingly long. The fifth legs are much smaller than those of the female which they resemble in showing only one lamellar segment, armed with six short setæ. Length about 0·38 mm. No eye visible.

Occurrence. Washed from the sand of Kames Bay, Millport, September to December, 1934. Centre of abundance about half-tide level. Moderately common.

Remarks. The hastate setæ on the exopods of legs one to four appear to project backwards on some legs and forwards on others. Probably in life they project in a plane more or less at right angles to that of the other setæ and when flattened under the cover-slip fall either forwards or backwards. In a whole mount they appear to project backwards.

Family **CANTHOCAMPTIDÆ.**

The majority of the interstitial copepods belong to this heterogeneous family, the various attempts at classification of which have been reviewed by Gurney (1932) who suggests an arrangement in a number of evolutionary series. This arrangement has been followed in dealing with the remaining copepods all of which appear to belong to this family. The first is included in Gurney's " Tetragoniceps Series " and the rest in his " Evansula Series," to which must be added Paraleptastacus Wilson and the two new genera described below.

Genus LEPTOPSYLLUS T. Scott.

Syn. Emertonia Wilson, 1932. Bull. 158. U.S. Nat. Mus., p. 256.

Body somewhat depressed, last segment of the metasome narrower than the preceding segments. Urosome more or less tapering posteriorly ; 4-segmented in the female, 5-segmented in the male. Metasome segments clearly marked off from one another by deep indentations (except in the female of *L.* (*Emertonia*) *gracilis*). Caudal rami elongate. Rostrum short and ill defined basally. Antennule 7- or 8-segmented, bearing a long æsthetasc on the fourth segment. Antenna 3-segmented ; the first two unarmed, the third with a number of terminal geniculate spines and one or two short lateral spines ; a 1-segmented exopod is attached distally to the basal segment and bears lateral and terminal setæ. The upper lip is obtusely conical and unarmed. The mandible has a well developed palp with a 1-segmented exopod. The maxillule, maxilla and maxilliped are normal. The basipod in legs one to four is large and expanded laterally, causing the whole of the exopod to project beyond the lateral margin of the metasome. Both rami of first legs 1- or 2-segmented. Exopods of legs two to four 3-segmented, endopods 1- or 2-segmented. Fifth legs 2-segmented. A single egg-sac is present.

Remarks. In 1894 T. Scott described a new copepod, taken from the shores of the Firth of Forth, which he named *Leptopsyllus typicus.* Three more species were described by T. and A. Scott in 1895, *L. intermedius* (1895a) from " pools near low-water on the shore at Musselburgh, Firth of Forth," and *L. robertsoni* and *L. minor* from the same situation and habitat (1895b). In 1900 Thompson and Scott described a fifth species, *L. herdmani,* obtained from " holes dug in the sand . . . at Port Erin," from which also they recorded *L. intermedius.* This latter species, it has been suggested by Sars (1911, p. 425), should be transferred to the genus Paramesochra. The two species of Leptopsyllus described below were at first thought to belong to Emertonia (Wilson, 1932) and they are undoubtedly congeneric with *E. gracilis* of that author. One of the species found here is, however, *L. minor* which, with *L. herdmani,* has previously been recorded from this district by T. Scott (1901). All of the seven species of Leptopsyllus grade one into the other and it is with some difficulty that *Paramesochra dubia* is separated.

Leptopsyllus constrictus sp. n. (Figure 2).

Female. In general structure it resembles *L.* (*Emertonia*) *gracilis* except that it is deeply constricted between the metasome segments. The antennule has only seven segments and the second segment is without a spine. The antenna is 3-segmented, with a 1-segmented exopod attached to the basal segment and bearing one lateral and one terminal spine. The upper lip is unarmed. The mandible palp shows two segments, the distal one with three terminal and one lateral seta, the basal segment having two lateral setæ and bearing the 1-segmented exopod tipped with two setæ. The maxillule shows a basal portion armed distally with teeth, and three lobes tipped with setæ. The maxilla appears to have three segments. The maxilliped has a short basal segment, a longer second segment and a very short terminal segment bearing a short curved claw and two accessory setæ. The exopod of the first leg has two segments and the endopod consists of one long slender segment bearing two small spines terminally. Both rami of the second, third and fourth legs show small differences from *L.* (*Emertonia*) *gracilis* in the number of spines and presence of hairs. The setæ of the fifth legs are not plumose and have not the same relative length as in that species. A single egg-sac is carried, with two eggs side by side and occasionally also a third placed transversely. The caudal rami are long, slightly tapering and bear each one long and one short terminal seta and a short plumose seta terminolaterally, with one inner and one outer marginal seta. The short terminal seta bears three or four long delicate hairs. Length about 0·32 mm.

Male. Resembles the female in the shape of the body but is more slender. The antennule is 7-segmented with an æsthetasc on the fourth. The exopod of the first leg has two segments and the endopod only one. The remaining legs resemble those of the female but are smaller. The anal segment is slightly smaller than in the female. Length about 0·30 mm.

Occurrence. Washed from the sand of Kames Bay, Millport. Very common just above low-water neaps.

Remarks. Though there is no doubt about there being two segments in the exopod of the first leg, in which it differs from *L.* (*Emertonia*) *gracilis*, it is possible that the endopod should be interpreted as having two segments in conformity with all the other species of the genus. There is a constriction at the end, particularly noticeable in the male, which may be true segmentation, but owing to its very small size it has not been possible to determine this with accuracy. An eye is present in this species and can be seen if the specimens are examined immediately after fixation. It disappears very rapidly.

Leptopsyllus minor T. and A. Scott (Figure 3).

Female. Body very much as in *L. constrictus*, with a large cephalosome and 4-segmented urosome. The anal segment is about half the length of the pre-anal segment. The caudal rami are long and somewhat fusiform in shape, bearing each a single short terminal seta, swollen basally, with a short spine on either side and three other setæ. The rostrum is small and sharply pointed. Antennule 7-segmented, the basal segment unarmed and the remaining segments more or less setose; there is a slender æsthetasc on the fourth segment. The antenna consists of three segments; the basal segment bears a 1-segmented exopod which has two lateral and one terminal seta; the second segment has a single lateral seta and the terminal segment has one lateral seta and several setæ and geniculate spines terminally. The upper lip is like that of *L. constrictus*. The mandible palp consists of a large basal segment with two smaller segments terminally, armed with setæ, and a 1-segmented exopod tipped with two setæ. The maxillule has only two distal lobes. The maxilla has two small endites on the basal portion not present in *L. constrictus*. The maxilliped is typical. The rami of the first leg are 2-segmented;

the segments of the exopod are sub-equal, the first with two small spines and a long distal seta, the second with four unequal terminal setæ; the endopod has a long unarmed basal segment and a short terminal segment

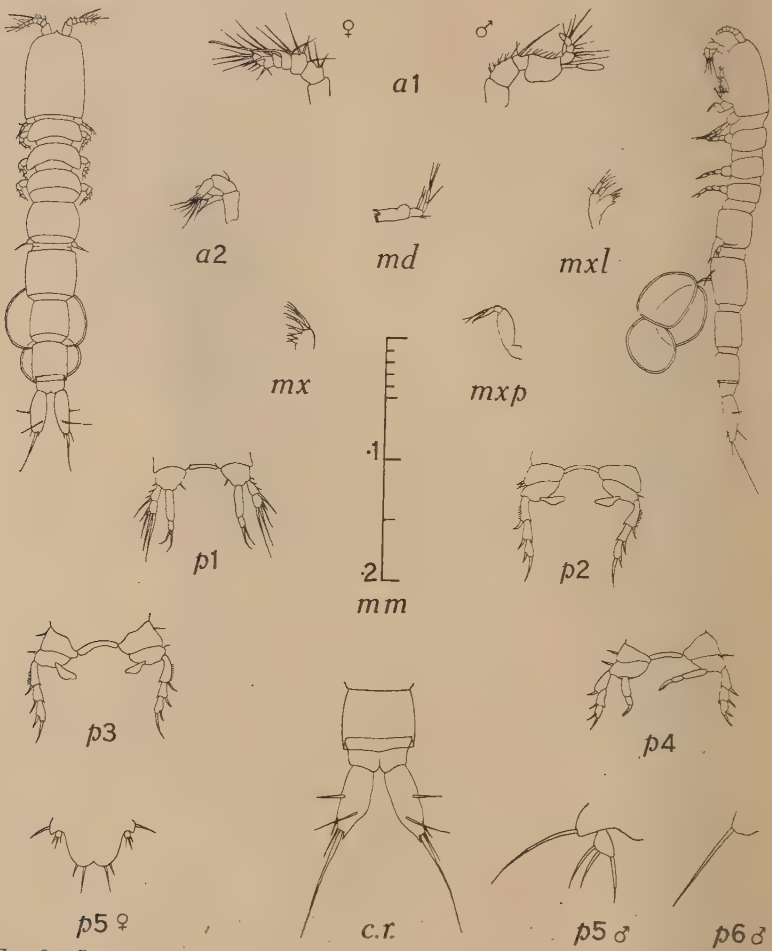

Fig. 3.—*Leptopsyllus minor* T. and A. Scott. Lettering as in Figure 1. Fifth and sixth legs of the male drawn to a scale 2·3 times that of the other appendages.

tipped with two unequal slightly clawed setæ. The second and third legs have 3-segmented exopods, and 1-segmented, unarmed, fusiform endopods. The exopods of the fourth legs are normal but the endopods are 2-segmented and well developed, the terminal segment bearing a curved spine. The basal segments of the fifth legs are considerably elongated and completely fused in the midline, bearing the usual lateral seta, and two terminal setæ ; the terminal segments are small and inconspicuous bearing three unequal setæ. The sixth legs are represented by a pair of short setæ. There is a single egg-sac, containing two or three eggs loosely held together and ovoid in shape.

Male. Resembles the female in general structure but has a 5-segmented urosome. Antennule 7-segmented, the fourth segment bearing a peculiar, apparently 2-segmented æsthetasc, the terminal portion of which is fusiform and the whole much shorter than is usual. The mouth parts and swimming legs are like those of the female. The fifth legs have a basal segment with one lateral seta, and the terminal segment has three setæ. The sixth legs consist of small lamellæ bearing each a single long seta.

Occurrence. Washed from the sand taken just above low-water neaps in Kames Bay, Millport, and found only between 3 and 10 cm. deep in the sand. Not very common.

Remarks. This species resembles *L. constrictus* in some features, but the two are easily separated on the structure of the caudal rami and by the extraordinary separation of the segments on fixation, such as has not been found with any other copepod from this fauna, although apparent in the drawings of Leptopsyllus made by T. and A. Scott. It is presumed that this feature is unnatural and therefore no measurements are given, but the animals are approximately the same size as *L. constrictus* (0·3 mm.). The æsthetasc in the male is peculiar as are also the fifth legs of the female and the first and fourth legs in both sexes.

Genus Paraleptastacus Wilson.

Paraleptastacus espinulatus sp. n. (Figure 4).

Female. Body elongate, cylindrical ; segments more or less equal in size. Urosome 4-segmented, not clearly separated from the metasome. Rostrum small and fused with the cephalosome. Antennule 7-segmented, the second segment the longest and the fourth bearing a moderately long æsthetasc. The antenna is 3-segmented with a small 1-segmented exopod attached near the centre of the second segment. The mouth parts are like those of *P. spinicaudus* (Figure 5). Exopods of the swimming legs are 3-segmented, the endopods 2-segmented. The fifth legs are 2-segmented ; the basal segment with the usual lateral seta and two short terminal setæ ; the terminal segment with one terminal and three lateral setæ. Caudal rami short, tapering terminally to end in a spine, and bearing one long and one short terminal seta and two lateral setæ. Egg-sac single with two or three large eggs one behind the other. Length about 0·40 mm.

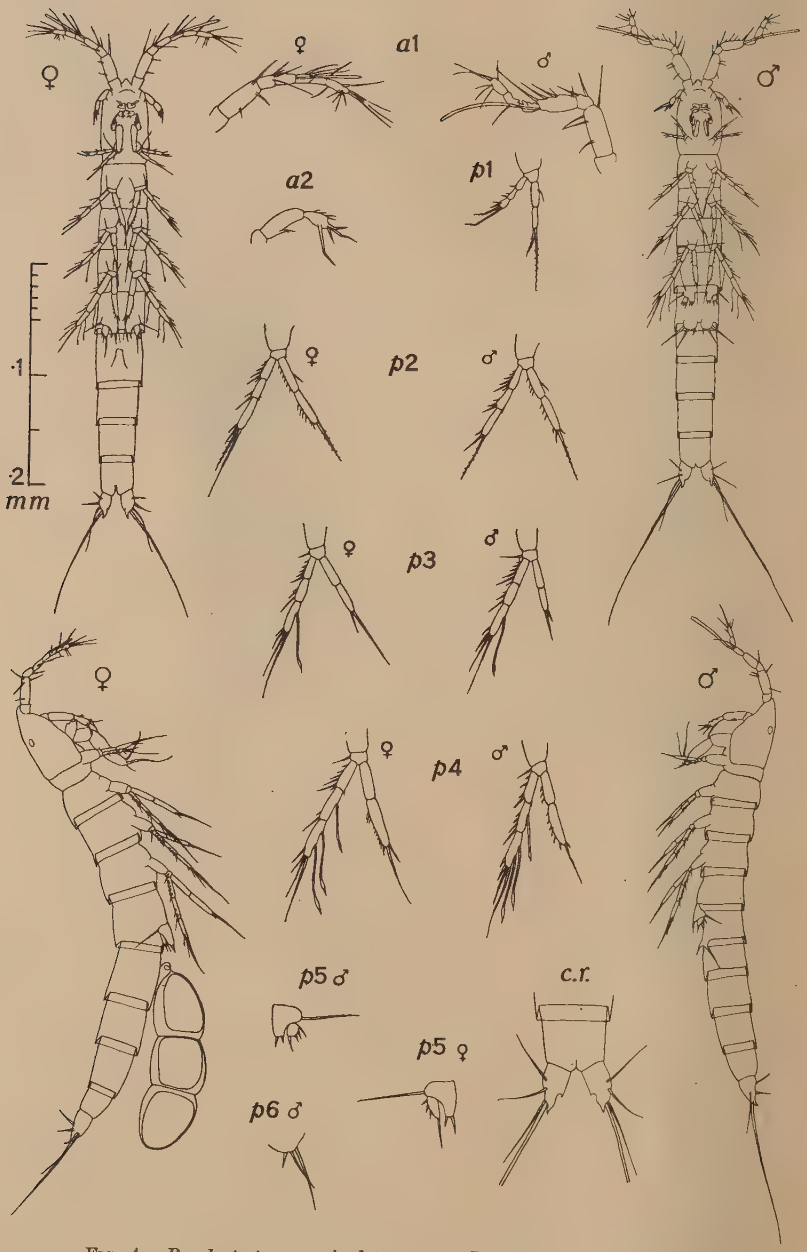
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FIG. 4.—*Paraleptastacus espinulatus* sp. n. Lettering as in Figure 1.

Male. Body of similar shape to that of the female but slightly shorter and with 5-segmented urosome. Antennule 7-segmented, twice geniculate and bearing a long æsthetasc on the fourth segment. Mouth parts as in the female. The swimming legs, except for the first, show small differences in spinulation from those of the female. The terminal segment of the fifth legs is longer than in the female and bears a long terminal seta. The sixth legs are small lamellæ each bearing one lateral and two terminal setæ. Length about 0·37 mm.

Occurrence. Very abundant in the sand of Kames Bay, Millport; generally distributed in the lower half of the Bay. Breeding from January to December.

Remarks. In its main features this species differs little from those described by Wilson (pp. 248–252). The anal segment is, however, nearly as long as the penultimate segment and the caudal rami are as long as the anal segment. In the proportions of these parts and in the number and arrangement of the setæ on the caudal rami this species resembles the male of *P. katamensis,* lacking, however, the large inner distal spine. A single median reddish eye is present. The antennules show differences in the number and arrangement of the setæ and the æsthetasc extends slightly beyond the end of the appendage in the female and well beyond in the male. The second segment of the exopod of the first leg bears two spines and similar small differences in the number of spines are seen in the second, third and fourth legs. A notable difference is in the number of hastate setæ on the exopods of the third and fourth legs. The third leg bears one on the inner side of the terminal segment and the fourth legs bears one on the second segment and two on the terminal segment. Male and female are alike in this respect. The distal segment of the fifth legs in the female bears only three lateral setæ. The setæ of the legs of both sexes of this species are practically devoid of spinules and the setæ of the caudal rami entirely so, upon which fact depends the choice of specific name. This feature and the number of hastate setæ on the third and fourth legs serve to distinguish this species from those previously described.

Paraleptastacus spinicaudus (T. and A. Scott) (Figure 5).

Syn. *Mesochra spinicauda* T. and A. Scott, 1895. Ann. Mag. Nat. Hist., Ser. 6, Vol. XV, p. 52, pl. V, Figures 12–25.
Leptastacus spinicaudus Sars, 1911. Crustacea of Norway. Vol. V, Copepoda (Harpacticoida), p. 417.

Apart from the very clear-cut difference in distribution, the main structural difference between this and the preceding species lies in the caudal region. The rami are shorter and stouter than in *P. espinulatus*

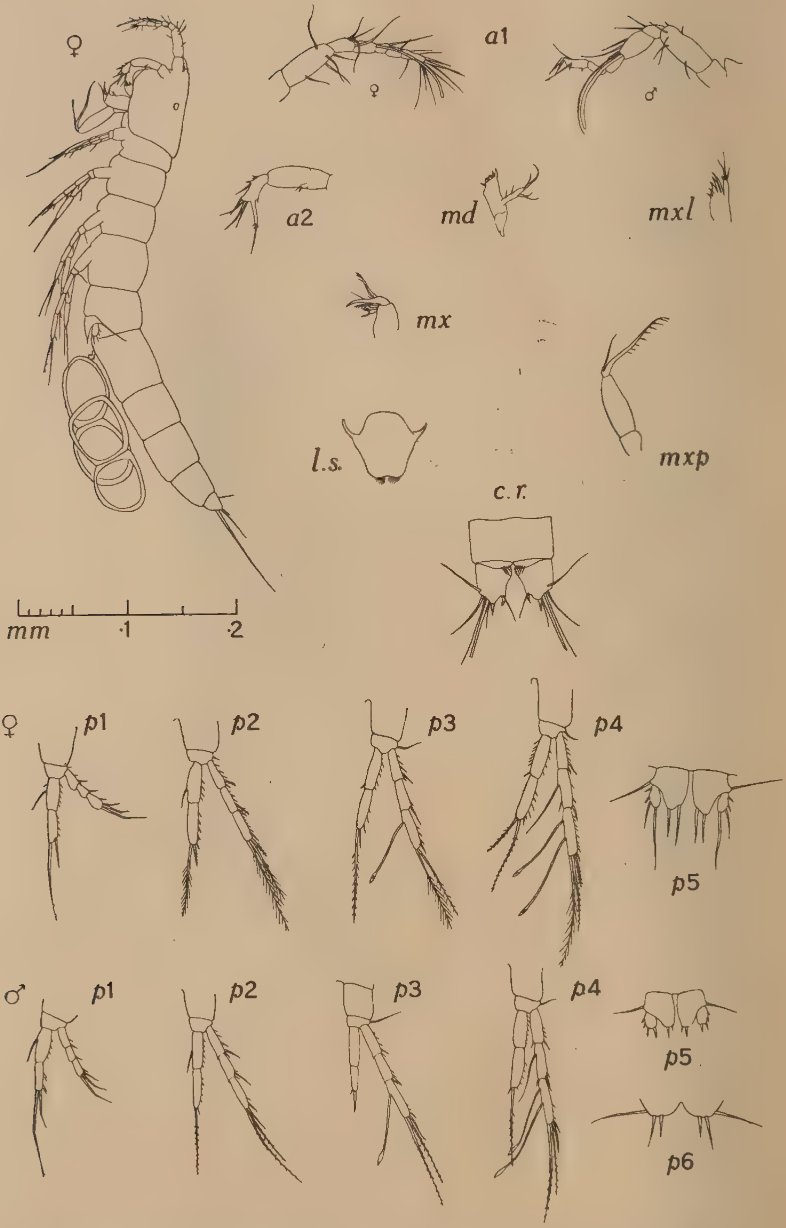
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FIG. 5.—*Paraleptastacus spinicaudus* (T. and A. Scott). Lettering as in Figure 1.

and bear more setæ and spines, and there are two well defined opercular tufts of setæ. There are also differences in the spinulation of the legs. The hastate seta on the second exopod segment of the fourth leg in *P. espinulatus* is replaced in this species by a long unarmed seta. The remaining setæ on the legs of this species are strongly denticulate or plumose. Length of female about 0·43 mm., of the male about 0·40 mm.

Occurrence. Washed from the sand of Kames Bay, Millport. Distribution very local, just below high-water neaps ; also in sand from the head of Loch Fyne.

Remarks. The genus Paraleptastacus was established by Wilson (1932) to include two forms obtained by him from sand washings. As pointed out by him it differs from Leptastacus in the structure of the antennules, the maxillæ, the fifth legs and the caudal rami. The species described above conform to the generic diagnosis given by Wilson in all but the maxillæ, in which they resemble Leptastacus. This difference, though noticeable, does not seem to warrant a new genus.

P. spinicaudus, originally described as *Mesochra spinicauda*, by T. and A. Scott (1895a) and later removed to the genus Leptastacus by Sars (1911, p. 417), was at first thought to be a new species. Specimens obtained from sand at the head of Loch Fyne in September, 1934, in relatively the same position above low-water as those in Kames Bay, while showing no important structural difference from the latter, were larger (0·5 mm.), had larger egg-sacs containing six or seven eggs, and appeared to be identical with *M. spinicauda* of T. and A. Scott.

The sand in which these specimens were found was of a coarser texture than that of Kames Bay and possibly the larger size and larger egg-sac may be correlated with the larger sand grains which would provide greater interstitial space. T. and A. Scott give no data upon which their measurements were based, and if the extended antennules are included in the measurements, the size of the Loch Fyne specimens agrees exactly with that given by them. Moreover their specimens were "in pools near low-water on the shore" and it appears almost certain that the copepods are identical.

Genus LEPTASTACUS Scott.

Leptastacus laticaudatus sp. n. (Figure 6).

Female. Body cylindrical, metasome and urosome not clearly demarcated. Antennule 7-segmented, with a long æsthetasc on the fourth segment. Antenna 2-segmented, with a 1-segmented exopod attached near the base of the basal segment. The upper lip bears two spines and six setæ. The mouth parts resemble those of *L. macronyx*, except for the maxillule, the structure of which was not clearly determined. Legs one to

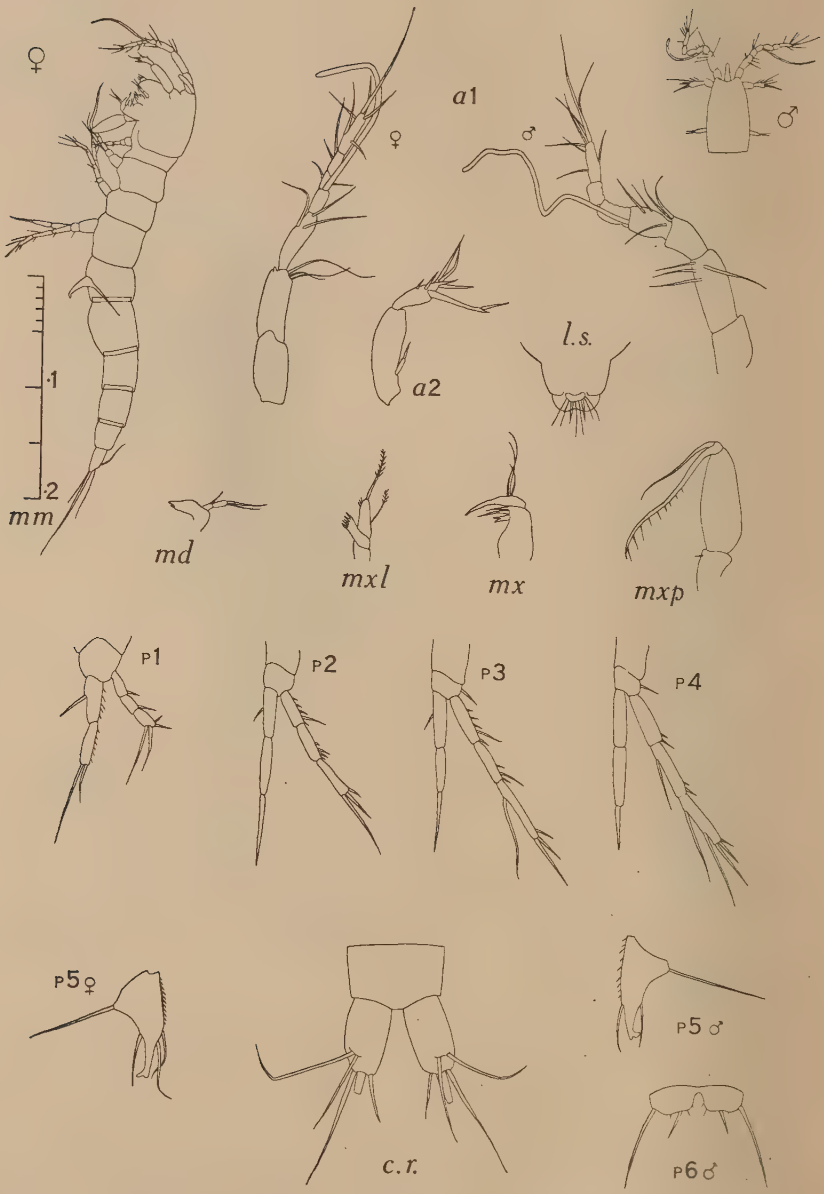
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FIG. 6.—*Leptastacus laticaudata* sp. n. Lettering as in Figure 1. Appendages drawn to a scale 2·8 times that of the adult.

four are as in *L. macronyx*, with minor differences in the arrangement of setæ and relative lengths of segments, particularly in the first leg. The fifth legs are of the same general shape as in the type but are expanded terminally, somewhat resembling a human foot. The caudal rami are short, scarcely exceeding the length of the anal segment and about half as wide as long ; each bears one long terminal seta with a shorter seta on either side, and two setæ on the upper surface. There is a single egg-sac containing two or three eggs. Length about 0·36 mm.

Male. This is shorter and more slightly built than the female and shows the usual modification of the antennules. The fifth legs are like those of the female but lack one seta, and a pair of lamellar sixth legs occurs armed laterally with one long seta and terminally with one short seta and three small spines. Length about 0·33 mm.

Occurrence. Thirty-six specimens were washed from sand at about half-tide in Balloch Bay, Isle of Cumbrae, in March, 1935. The majority occurred above 2·5 cm. and none was found below 5 cm.

Remarks. This species differs from *L. macronyx* mainly in the fifth legs and the caudal rami. These features, supported by the difference in distribution, appear to warrant a new species. *L. macronyx* was dredged from 14 fathoms on a clean sandy bottom, whereas *L. laticaudatus* occurs at about half-tide in somewhat muddy sand.

Genus PSAMMASTACUS gen. n.

Body elongate, cylindrical, widest at the second metasome segment, and gradually tapering posteriorly. Cephalosome about equal to the first two metasome segments. No definite demarcation between metasome and urosome. Caudal rami about half as long as the anal segment and little longer than wide. Rostrum prominent, curved and well defined. Antennule 6- or 7-segmented, twice geniculate in the male, and bearing a long slender æsthetasc on the fourth segment. Antenna 3-segmented, the second segment showing no sign of division but bearing the rudimentary exopod near the middle. Upper lip prominent. Mandible with simple 2-segmented palp. Maxillule armed with numerous spines and setæ. Maxilla and maxilliped similar to those of Paraleptastacus. First leg with 1-segmented exopod and 2-segmented endopod. Remaining swimming legs with 3-segmented exopods and 2-segmented endopods. Fifth legs in both sexes reduced to simple lamellæ. Sixth legs present in both sexes and of similar structure to the fifth pair. Egg-sac single, with two or three eggs one behind the other.

Remarks. This genus is distinctive in its upper lip, but the remaining mouth parts all resemble those of copepods of the Evansula Series

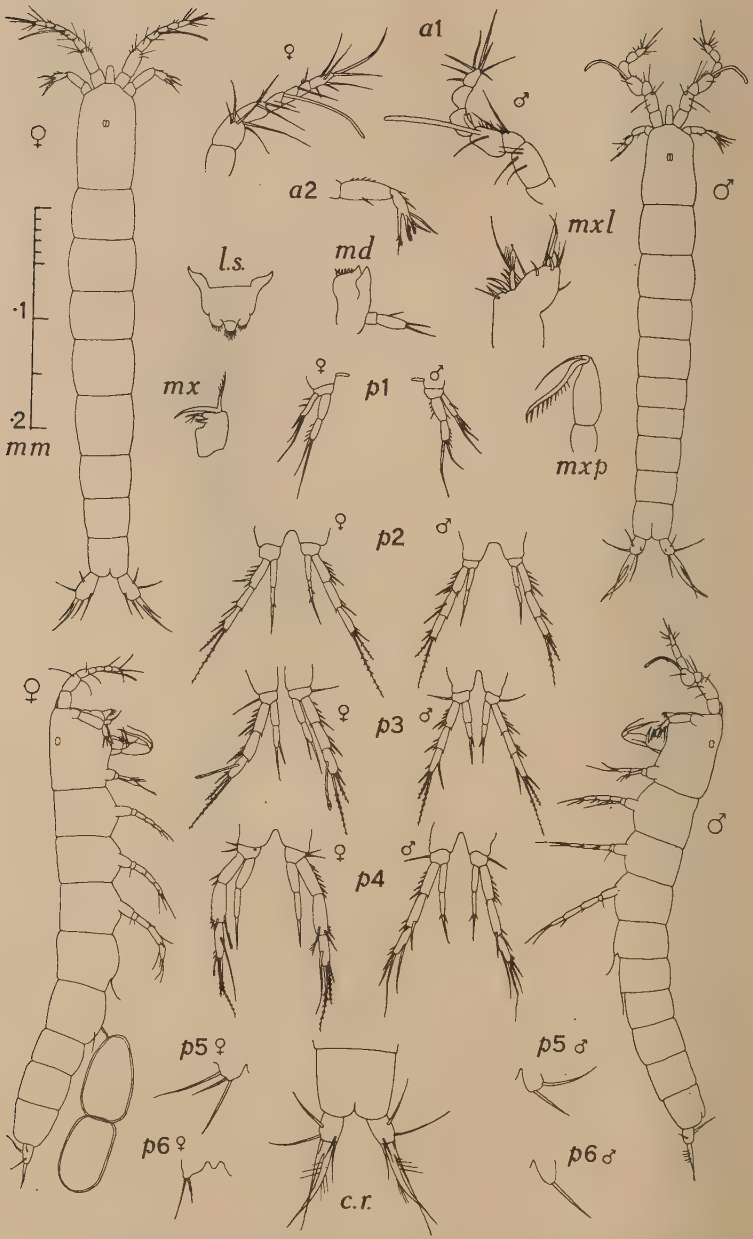
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FIG. 7.—*Psammastacus confluens* gen. n., sp. n. Lettering as in Figure 1. Mandible and maxillule drawn to a scale 2·3 times that of the other appendages.

(Gurney, 1932). The first legs are peculiar but the others, including the fifth pair, are similar to those of the copepods of this Series.

Psammastacus confluens sp. n. (Figure 7).

Female. Cephalosome about equal to first two metasome segments. Rostrum longer than the first segment of the antennule. Reddish eye present in fresh specimens. Antennule 7-segmented, the second segment the longest. Antenna with exopod represented by a single seta attached about the middle of the second segment which has a fringe of fine hairs on the opposite margin; terminal segment with three denticulate spines and two setæ terminally, and three short spines laterally. Upper lip trilobed, each lobe with a tuft of fine hairs. Mandible with 2-segmented palp, the second segment having two terminal and one lateral seta. Maxillule consisting of a basal portion bearing spines and setæ and a distal lobe similarly armed. Maxilla normal. Maxilliped 2-segmented, the basal segment unarmed; the terminal segment with one long curved claw, bearing a number of long spines and an accessory curved seta. First leg with 1-segmented exopod bearing two short spines externally, and tipped with three unequal setæ. Endopod 2-segmented, the end segment tipped with two long unequal setæ and with a fringe of short hairs on the inner margin. Second, third and fourth legs with 3-segmented exopods and 2-segmented endopods. The first two segments of the exopod with a varying number of hairs and spines on the outer margin and, in the fourth leg, one inner seta bearing a fringe of fine hairs, on the second segment. End segments of exopods with two long denticulate setæ terminally and a spine and hairs on the outer margin. In the third leg the end segment bears one short hastate seta inside, replaced in the fourth leg by a long unplumed seta. The fifth and sixth legs are simple lamellæ bearing three setæ in the fifth pair and two in the sixth. The caudal rami are short, stout structures attached to the ventral part of the anal segment, making a break in the continuous line of the dorsal surface. Each ramus is armed with two apical setæ, fused for a short distance proximally, with one short seta inside and a longer one projecting laterally; there are also two dorsal setæ. Length about 0·48 mm.

Male. Similar to the female in general shape of the body but slightly shorter and more slender. Cephalosome shorter than the first two segments of the metasome. Antennule 7-segmented and twice geniculate, with a stout æsthetasc on the fourth segment; inner surface of the fifth segment with a rugosity for gripping. Mouth parts as in the female. The swimming legs are segmented like those of the female but show slight differences in spinulation. The fifth and sixth legs resemble those of the female but have only two and one seta respectively. The caudal rami are similar to those of the female. Length about 0·40 mm.

Occurrence. Washed from the sand of Kames Bay, Millport, at about high-water springs. Also found in the sand from the bed of the stream flowing through the Bay. Very common.

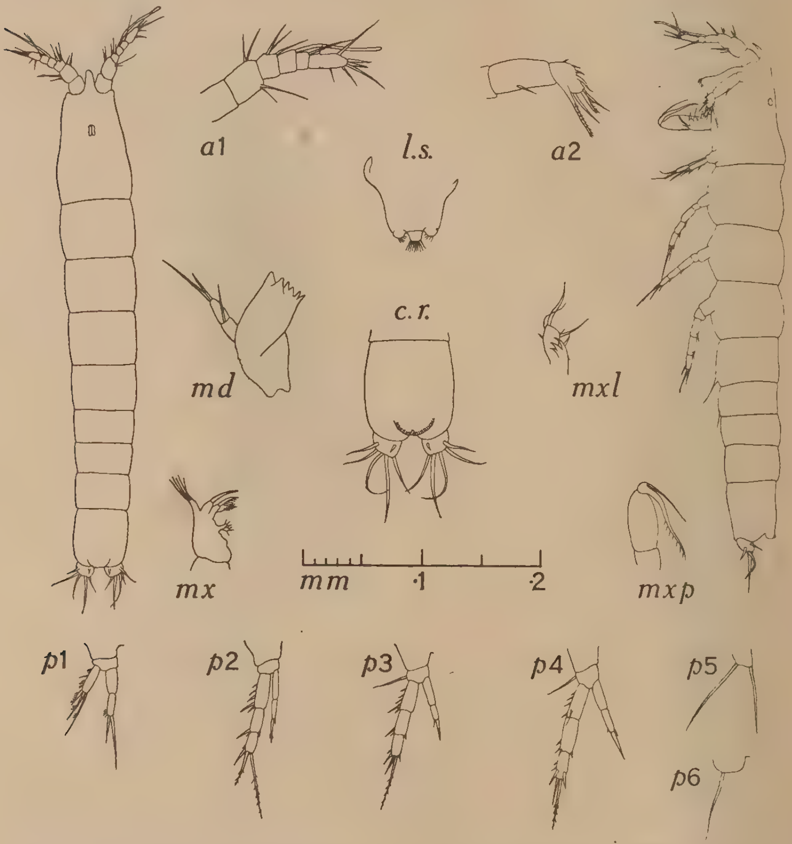

FIG. 8.—*Psammastacus brevicaudatus* sp. n. Lettering as in Figure 1. Mandible drawn to a scale 2·3 times that of the other appendages.

Remarks. The caudal rami are distinctive and resemble the description given in Monard's key (1927) for Marshia (now Cletocamptus). Herrick's (1895) figure of *M. albuquerquensis* also shows the apical setæ fused basally.

Psammastacus brevicaudatus sp. n. (Figure 8).

Female. Cephalosome about equal to the first two metasome segments. Rostrum large and curved. Eye conspicuous, reddish. Antennule 6-

segmented, the first two segments about equal and larger than the others; a short slender æsthetasc borne on the fourth segment. Upper lip prominent, trilobed. Mandible with 2-segmented palp; the first segment with one seta and the distal segment with two unequal terminal setæ. Remaining mouth parts as in *P. confluens*. Legs one to four with similar segmentation to those of *P. confluens* but with slight differences in setation (cf. Figures 7 and 8). Fifth and sixth legs simple lamellæ with two and one seta respectively. Anal segment large, with distinct crescentic operculum, fringed with fine hairs. Caudal rami very short, rounded, each bearing four short terminal setæ and two dorsal setæ. Egg-sac single, containing two or three eggs. Length about 0·43 mm.

Male. Unknown.

Occurrence. Washed from the sand of Kames Bay, Millport, at about high-water springs in association with *P. confluens*. Not very common.

Remarks. The caudal rami serve immediately to distinguish this species from the only other species so far described.

Genus Arenocaris gen. n.

Body long, cylindrical, widest in the middle. Cephalosome short; rostrum large, curved. Urosome 4-segmented in the female, 5-segmented in the male. Caudal rami elongate. Antennule 7-segmented, with long æsthetasc on the fourth segment, and twice geniculate in the male. Antenna 3-segmented, basal segment short; second segment with a suggestion of segmentation at the point of attachment of the short, 1-segmented exopod; third segment with one large spine and a number of shorter, geniculate spines terminally, and several short spines on the lateral margin. Upper lip fringed with hairs. Mandible with a small 2-segmented palp. Maxillule with a group of short curved spines and a lobe bearing spines and setæ. Maxilla of the usual Canthocamptid type. Maxilliped 3-segmented; basal segment with short inner spine; second segment unarmed; terminal segment with a long curved claw and a single seta. Both rami of first legs 2-segmented. Legs two and three with 3-segmented exopods and 1-segmented endopods. Fourth legs with 3-segmented exopods and stout, 2-segmented endopods, slightly modified in the male. Fifth legs 2-segmented, the terminal segment greatly reduced in the male. Sixth legs present in the male. Genital area in the female well developed and noticeably sculptured. Caudal rami about as long as the anal segment and each bearing one short, stout, apical seta and one similar lateral seta which projects at right angles to the body, giving a characteristic appearance. Eye invisible. Egg-sac single.

Remarks. This genus appears to fit naturally into the Evansula Series (Gurney, 1932, p. 49) and to link up with Stenocaris, supporting Gurney's

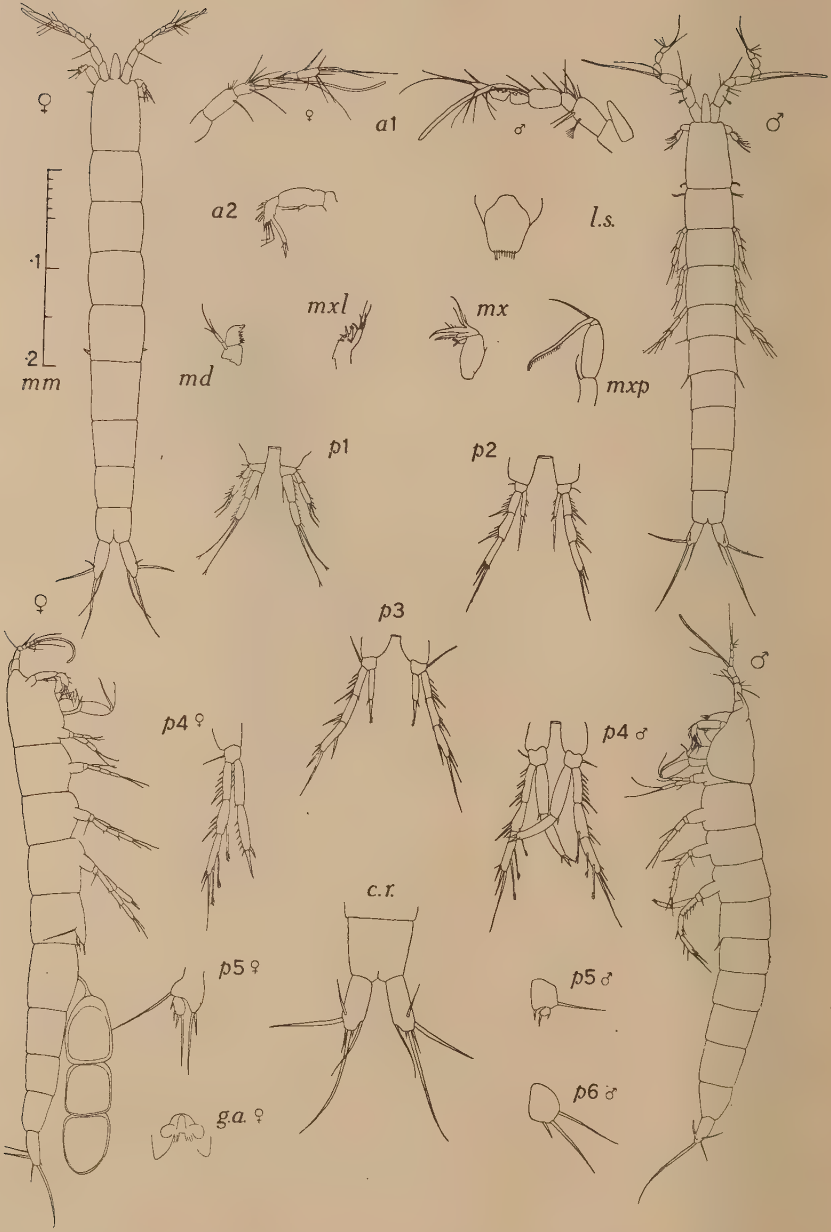
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Fig. 9.—*Arenocaris bifida* gen. n., sp. n. *g.a.*, genital area; other lettering as in Figure 1. The caudal rami are those of the male.

suggested inclusion of that genus within this Series. In the general elongate shape of the body this genus resembles Stenocaris; in the structure of the antennules, antennæ, upper lip and other mouth parts it resembles Paraleptastacus. In the reduction of the endopods of the swimming legs it resembles Stenocaris, but in the structure of the first legs it is peculiar. The fifth legs do not show the reduction found in Stenocaris and Leptastacus, but resemble those of Paraleptastacus. The rostrum, however, is much larger and more clearly defined than in that genus.

Arenocaris bifida sp. n. (Figure 9).

Female. The body is widest in the fourth and fifth segments, tapers slightly anteriorly and somewhat more noticeably posteriorly. The large rostrum is well defined and ventrally curved. Antennule 7-segmented, the fourth bearing a long æsthetasc. The upper lip is prominent in lateral view. The exopods of the first legs bear lateral spines and two slightly bent terminal setæ. The endopods are fringed with hairs externally and the first segment bears a single seta about the middle of the inner margin; the second segment has two long setæ, distinctly bifid distally. This feature has given rise to the specific name. In legs two to four the first two segments of the exopods have each one long spine and a number of shorter spines and hairs on the outer margin; the third segment bears one long and two short terminal spines and in the third legs one short spine on the inner margin; in the fourth legs there are two modified setæ on the inner margin with a similar seta on the inner margin of the second segment. These setæ, which are relatively short and bear each a tuft of fine hairs distally, occupy positions similar to those of the hastate setæ in Paraleptastacus and Hastigerella, and both probably have a sensory function associated with the habitat. The endopods of legs two and three are 1-segmented and tipped with a single, more or less stout, spine which in the third leg also bears a tuft of fine hairs. The endopod of the fourth leg is 2-segmented, both segments being larger and more strongly built than the corresponding exopod segments; the terminal segment is tipped with one large strong spine and a smaller one; both segments are fringed with hairs externally. The fifth legs are of the usual 2-segmented type, the basal segment bearing two setæ terminally and a single long seta laterally; the terminal segment has one long and one short terminal seta and two short lateral setæ. The genital area is prominent and ornately sculptured. The caudal rami are almost as long as the anal segment; there is a single stout terminal seta and a second, equally stout, projecting laterally; a third seta occupies a dorsal position, while a fourth is situated internal to the main apical seta. There is a single egg-sac with two or three eggs carried one behind the other. Length about 0·53 mm.

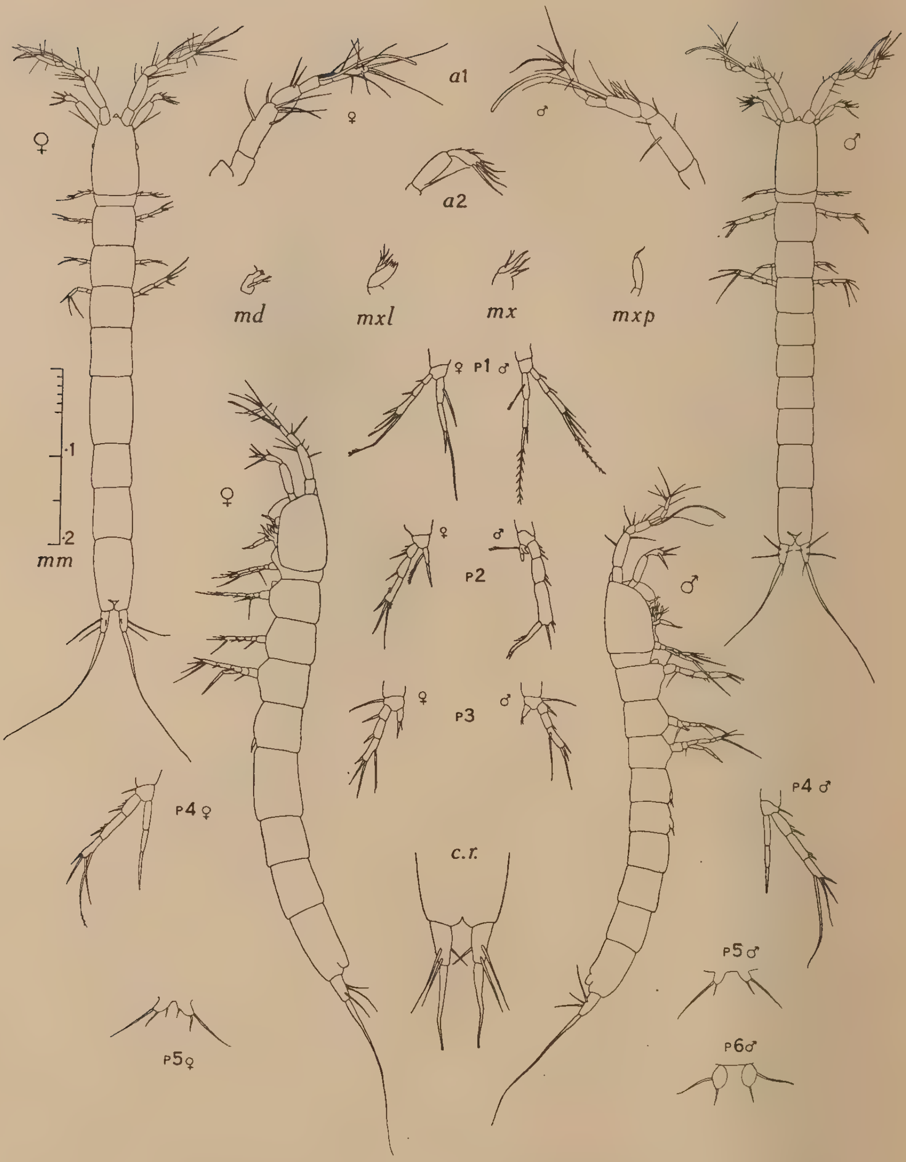
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FIG. 10.—*Stenocaris minuta* sp. n. Lettering as in Figure 1.

Male. Body similar to that of the female but more slender and with 5-segmented urosome. Antennules 7-segmented, twice geniculate, with a long æsthetasc, stouter than that of the female, on the fourth segment; the fifth and sixth segments are corrugated on their inner margins and presumably provide a gripping surface when closed. Mouth parts as in the female. First three pairs of legs like those of the female with slight differences in the number of small spines and hairs, but these are of little importance since similar differences are seen in the two members of any one pair of legs. The fourth legs have endopods of similar structure to those of the female but they are even more stoutly built and have two short spines terminally, with one smaller spine; there is a single short spine distally on the outer margin of the second segment; the whole ramus is somewhat curved. The fifth legs are smaller than those of the female and the terminal segment is very small with only three short setæ. The sixth legs are represented by lamellar plates each bearing the usual long lateral seta and two terminal setæ. The caudal rami are as in the female but have in addition two small setæ situated one on either side of the apical seta. Length about 0·46 mm.

Occurrence. Washed from the sand of Kames Bay, Millport, and found only in a restricted area at about half-tide level. Not very common.

Genus STENOCARIS Sars.

Stenocaris minuta sp. n. (Figure 10).

Female. Body cylindrical, the 4-segmented urosome showing no demarcation from the metasome. The genital and anal segments are about equal, longer than any other segment but slightly shorter than the cephalosome. Rostrum small, well defined basally. Antennule 6-segmented, with an æsthetasc on the fourth. Antenna 3-segmented, the 1-segmented exopod attached basally to the second segment and bearing a single long seta. Mouth parts typical. Exopods of first four pairs of legs 3-segmented; endopods of first and fourth pairs 2-segmented, of second and third pairs 1-segmented. Fifth legs small lamellæ bearing three unequal setæ. Caudal rami equal to one-third of the length of the anal segment, narrow and tapering, armed with one long slender terminal seta and three lateral setæ. No specimens were obtained with egg-sacs which are presumably paired as in other members of the genus. Length about 0·60 mm.

Male. Body shorter and narrower than that of the female, with 5-segmented urosome. Antennule 7-segmented, geniculate between the fifth and sixth, and bearing a relatively long æsthetasc on the fourth. Mouth parts as in the female. The first and fourth legs resemble those of the female. The exopod of the second leg is 3-segmented and stoutly built, the terminal segment bearing a long stout seta ; the endopod is 2-segmented, the basal segment armed with one lateral seta internally and a short hook externally ; the terminal segment is rounded and unarmed. The third leg has a 3-segmented exopod and a 1-segmented endopod, conical in shape and slightly constricted in the middle and armed terminally with two short spines. The fifth and sixth legs are simple lamellæ bearing each two setæ. Length about 0·50 mm.

Occurrence. A small number of specimens of this copepod was obtained from a sample of coarse sand collected at the head of Loch Fyne in September, 1934.

Remarks. This species differs from *S. gracilis* Sars in having the basal segment of the antenna distinctly divided, and in the relative lengths of the rami and segments of the swimming legs. The fifth leg is also much reduced. It differs from *S. minor* (Scott) in having only six segments in the antennule of the female, and in the structure of the caudal rami. It is, moreover, considerably smaller than either of these species.

It is a pleasure to acknowledge here my indebtedness to Dr. R. Gurney for advice on the systematic position of some of the species herein described.

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Plankton Production and its Control.

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The Plymouth Laboratory of the Marine Biological Association.

With 16 Figures in the Text.

INTRODUCTION.

THE plant population at stations extending in a line seaward from Plymouth Breakwater had been surveyed in 1933 by means of a measuring net (Harvey, 1934) and estimated from its pigment content. It was desired to extend the scope of this to include a quantitative survey of the zooplankton, to test the broad conclusion arrived at that the plant population is regulated by the intensity of grazing by animals, and to compare the estimated plant population with actual counts of plant cells.

In order to compare the magnitudes of the plant population from time to time with the animal population supported by it, and to estimate the quantity of vegetation produced by the plant population, it is necessary to follow the changes in some element which is a common constituent of plants, animals, and the water.

Accurate methods of analyses were available both for the phosphorus content of the total plankton caught and for the phosphate in the water, but no method of sufficient accuracy is yet available for the phosphorus in dissolved organic substances in the water. Since these may, and probably are, being continuously added to and continuously breaking down to phosphate, we are not able to follow the whole phosphorus cycle. Nevertheless it was thought that data concerning this constituent in the water and in the plankton would best repay further and more detailed investigation.

Although Station L4, 5 miles beyond the breakwater, is not beyond the influence of land, the phytoplankton was in 1933 typical of the offshore flora. For this reason, and because it is accessible, it was decided to follow the seasonal changes there.

The routine employed was to make several vertical hauls between the surface and 45 metres—the depth being about 50 metres—a measured quantity of water, usually about one cubic metre, passing through the silk net. Formalin was immediately added to the catch, and aliquot portions filtered for estimation of pigment and of phosphorus content of the plankton, other portions being kept for counting the animals and plants. At the same time water samples were taken from various depths for the estimation of the phosphate and salt content of the water, and determination of the temperature.

Figure 1 shows the number of animals caught per cubic metre of sea on the various occasions throughout the year when observations were made. It also shows the units of plant pigments in the phytoplankton caught in the net per cubic metre of sea. It is noticeable that the changes in plant population are much greater and more sudden than the changes in the animal population.

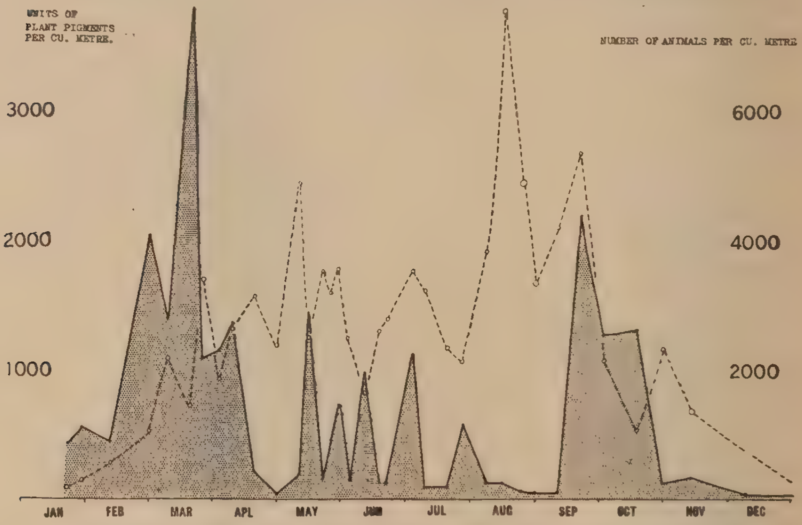

FIG. 1.—Points joined by continuous line represent the units of plant pigments per cubic metre of water, in the water column between surface and 45 metres at Station L4. Circles joined by dotted lines represent number of animals per cubic metre. The lines joining the points and circles have no real significance. Year 1934.

THE GENERAL HYDROGRAPHIC CONDITIONS.

In order to interpret the changes in plant and animal population through the year, it is necessary to consider, at least, movements of the water into and out of the area, also the seasonal changes in both temperature and available nutrient salts.

Concerning the first we have little definite knowledge. The position L4 lies outside the belt of inshore water which is considerably diluted by run off from the land and has a different type of seasonal change in flora from offshore waters. It lies inside the northern edge of an area of water, gradually increasing in salinity and depth to the southward, which is not usually subject to considerable or rapid changes. Further to the southward, 50 or more miles distant from L4, variable and temporary inflows of water from the Atlantic are most apparent, but on occasions these changes extend further north. The water occupying the L4 area does not remain there all the year round. Marked changes in salinity sometimes take place and drift bottles, both surface and bottom, have been found to work up Channel and down Channel. Movements and changes are quite irregular, and it would require a close and extensive network of observations to follow them. Nevertheless it seems that, usually, the water entering the area has moved in from areas of similar depth where the plants and animals had been subjected to similar conditions. It follows that the samples taken at L4 may mostly be considered as chance samples of the flora and fauna over a more or less wide area where their conditions for growth have been similar.

This element of uncertainty is inherent in any such series of observations made at a position in the open sea, for movements of the water masses are everywhere taking place. On account of this, comparison of the seasonal changes in flora and fauna and of the conclusions drawn from them with similar data in a semi-enclosed area, less subject to such waterchanges, such as Loch Striven, are particularly useful.

In Figures 2 and 3 the changes in salinity and temperature of the water at L4 are shown. Full data will be published in the Bulletin Hydrographique for 1934.

The phosphate contents of water collected at L4 are shown, to the nearest milligram of phosphorus per cubic metre, on the lower diagram in Figure 4, while the curve above shows the integral mean content of the whole column of water from surface to bottom expressed in terms of mg. P per m^3.

The winter of 1933–1934 was unusual, there was less phosphate in the water than in some previous years, the quantities fluctuating irregularly.

During February, 1934, moving masses of water containing between 10 and 15 mg. P/m^3.—a rather low value for the time of year—occupied the area. During the latter part of the month, during March and early April, a decrease took place and the area became occupied with water containing 5 mg. P/m^3. We do not know that this mass of water occupied a similar coastal position subject to similar conditions for plant growth in February, but from its salinity this seems probable. We do not know that in February it contained a similar quantity of phosphate—10 to 15 mg. P/m^3—as the water then in the L4 area, but since this quantity is lower than usual in previous years, we can conclude that the phytoplankton had utilised at least some 6 mg. P/m^3. during the period of its spring flowering, and possibly as much as 8 mg. P/m^3.

From the middle of April until the middle of August there is a further fall in dissolved phosphate, amounting to some 3 mg. P/m³. During July a temporary increase occurred, perhaps due to the incursion of water richer in phosphate or perhaps indicating the beginning of regeneration ; further to seaward at E1 an increase in phosphate in the bottom waters has been observed during July (Atkins, 1926).

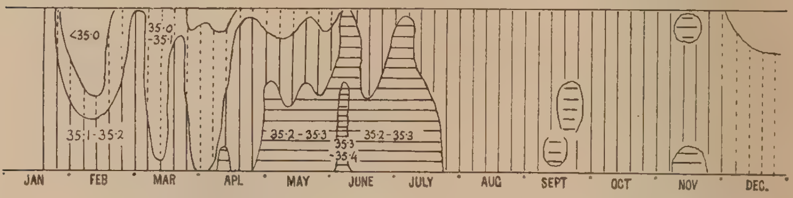

Fig. 2.—Isopleth diagram representing the changes in salinity of the water between surface and bottom at L4 during 1934.

During the latter part of August a rapid increase in phosphate took place as the rate of regeneration outstripped the rate at which phytoplankton was utilising it. This continued until the September outburst of diatoms which synchronised with a decrease in phosphate.

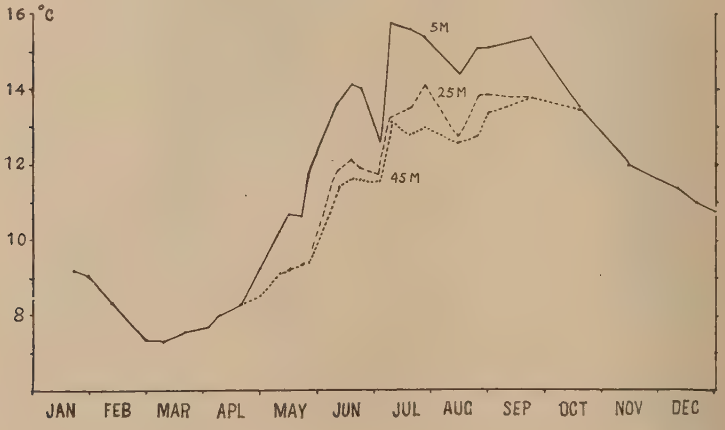

Fig. 3.—Temperature of the water at 5, 25 and 45 metres depth at L4 during 1934.

The estimations of dissolved phosphate were made by means of the Atkins-Denigès method with the modification that half the customary concentrations of acid and molybdate were used (Kalle, 1934). A correction has been applied for salt error, the observed concentrations of phosphate being multiplied by the factor 1·13, as found by Kalle using a photometer and confirmed here using direct visual colour comparison.

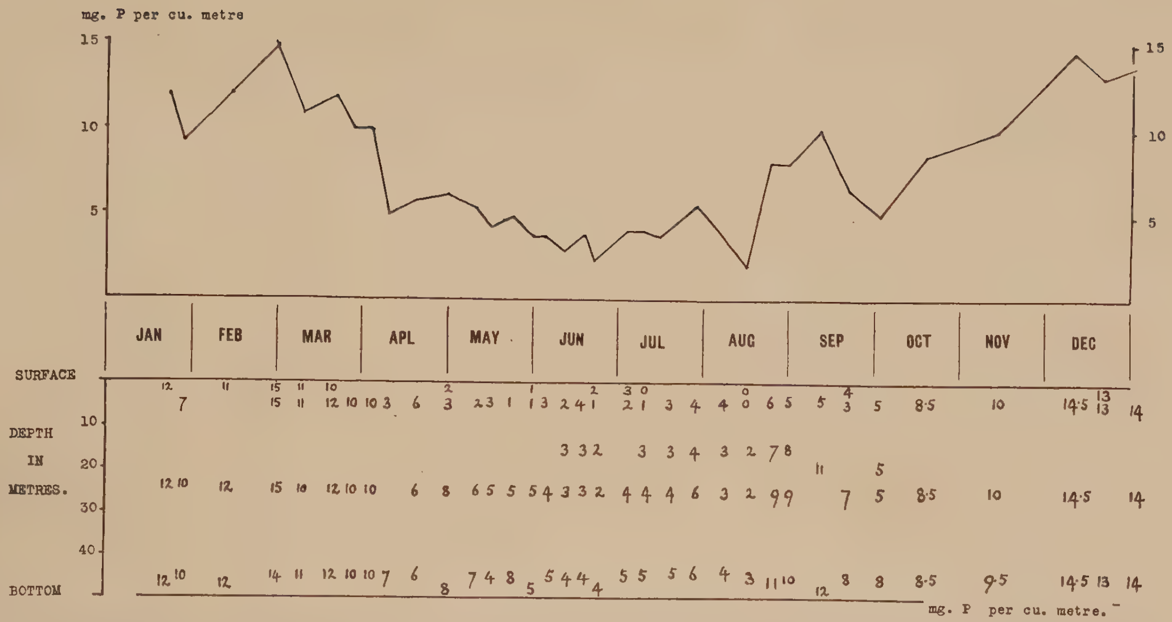

FIG. 4.—The upper curve shows the average phosphate content of the column of water between surface and bottom. The lower diagram shows the phosphate found in the various samples. In both the phosphate is expressed as mg. P per cubic metre.

The method of determining phosphorus in plankton has already been described (Cooper, 1934).

SEASONAL VARIATION IN ILLUMINATION.

The daily production of vegetation is dependent upon the day to day population of growing plants and the light energy available for photosynthesis over the 24-hour period. It is further influenced by temperature, by the concentration of nutrient salts, and it doubtless varies with the species of plants present, some diatoms being quicker growing than others. Of these factors the quantity of available light plays a marked and considerable part. Some knowledge of its change in magnitude during the course of the year is consequently necessary in order to interpret the data obtained during this survey.

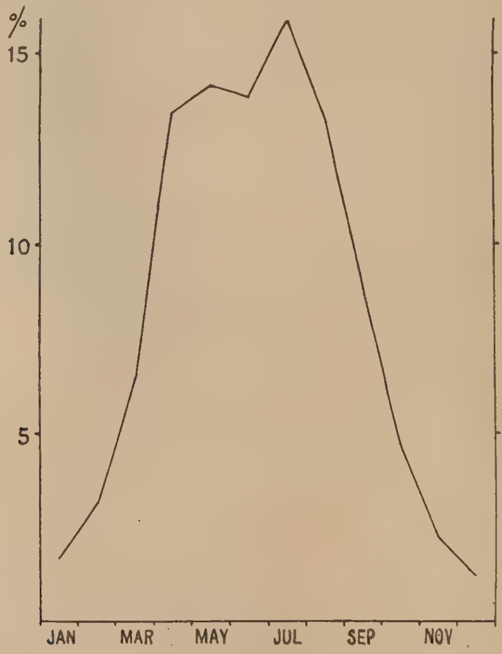

FIG. 5.—The points on the curve show for each month the percentage of the total illumination which fell throughout the whole year (W. R. G. Atkins).

During 1930 the light falling on the roof of this laboratory was measured, and the total illumination for each month is plotted in Figure 5 in terms of the total illumination during the whole year (Atkins, unpublished data). The curve is distinctive. A similar amount of light energy reaches the sea each month during April, May, June, July and August. This amount is nine times the amount reaching the sea in December and January.

It does not follow that the quantity of light available for photosynthesis in the sea is nine times more in summer than in winter. In a position such as L4 where the water is tolerably clear, about one-half of the light entering the surface penetrates to a depth of 5 metres, a quarter to 10 metres and an eighth to 15 metres. Hence the quantity of light penetrating below the 16 metre level in summer is comparable to the quantity entering the water at the surface in winter.

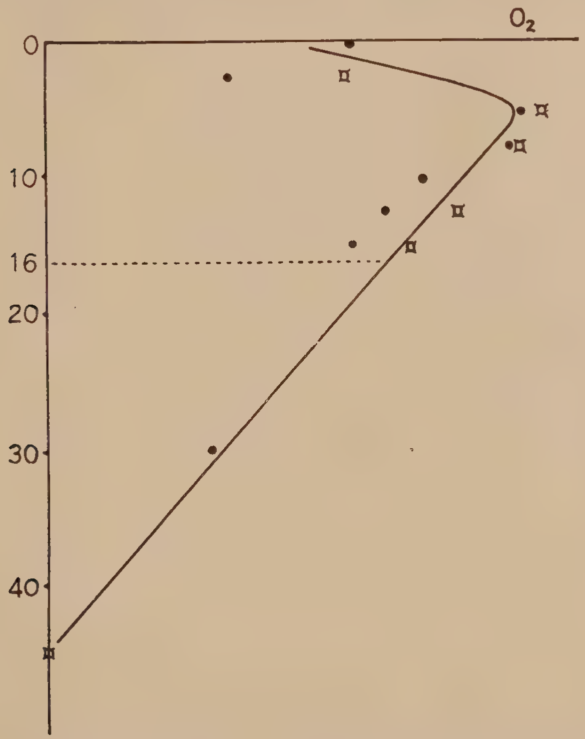

Fig. 6.—The points show the oxygen produced by a litre of diatom culture suspended in the sea at various depths over a period of 24 hours, July 12–13 and 19–20 (Miss P. M. Jenkin).

The production of vegetation, or plant material, by the same number of diatoms has been investigated over 24-hour periods in July at different levels in the L4 area (Miss P. M. Jenkin, private communication). This shows that if the diatom population was evenly distributed between surface and bottom the production of vegetation would be related to depth in the manner shown in Figure 6. With the diatoms used in the experiments

TABLE I.

	Jan.	Feb.	March.				April.		May.					
	29	12	1	9	20	26	3	20	1	10	15	23	25	30
Bacillaria paradoxa	240	396	2,483	340	1,035	–	228	–	–	–	–	–	–	–
Biddulphia mobiliensis	41	18	43	82	–	–	–	10	–	–	–	–	–	–
B. sinensis	97	103	576	516	1,200	288	307	–	–	–	–	–	–	–
B. regia	22	16	26	25	41	8	3	–	–	–	–	–	–	–
Chætoceros sp.	41	–	–	–	–	38	40	–	–	–	–	–	74	–
C. decipiens	50	–	–	139	1,415	262	218	–	–	–	–	–	–	–
C. danicus	–	4	6	3	41	8	3	–	–	–	–	–	–	–
C. didymus	–	27	–	14	233	–	–	–	–	–	–	–	–	–
C. densus	–	–	26	39	274	38	102	575	180	78	–	–	–	–
C. curvisetus	–	–	–	–	546	49	43	–	–	–	52	–	176	–
C. teres	–	–	–	–	71	16	13	–	–	–	–	–	–	–
C. debilis	–	–	–	–	37	–	–	–	–	–	–	–	–	–
C. convolutus	–	–	–	–	–	–	–	–	–	–	–	–	–	–
C. constrictus	–	–	–	–	–	–	–	–	–	–	–	–	–	–
C. laciniosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–
C. mitra	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Coscinodiscus excentricus	117	116	50	192	158	91	10	–	–	–	–	–	–	–
C. granii	13	9	30	–	25	–	–	–	–	–	–	–	–	–
C. radiatus	–	–	13	–	40	–	10	–	–	–	–	–	–	–
C. concinnus	–	–	–	10	12	4	–	–	–	–	–	–	–	–
Dytilium brightwelli	–	2	40	50	133	19	3	–	–	–	–	–	–	–
Eucampia zoodiacus	39	–	–	25	154	–	557	–	–	–	–	–	–	–
Gyrosigma sp.	2	–	–	10	–	–	10	–	12	–	7	–	–	–
Guinardia flaccida	52	64	153	210	675	163	382	5	–	–	520	115	55	354
Hyalodiscus stelliger	4	–	13	3	4	4	3	14	6	–	–	–	–	–
Nitzschia seriata	86	–	–	60	–	–	7	–	–	–	–	–	–	–
N. delicatissima	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Paralia sulcata	86	–	190	79	34	125	82	400	59	66	52	–	–	109
Rhizosolenia alata	2	–	20	–	96	23	100	67	6	–	15	–	–	–
R. alata, var. indica	–	–	–	–	–	–	–	–	–	–	–	–	–	–
R. shrubsolei	6	–	40	10	4	–	23	5	30	–	15,300	142	5,240	10,200
R. færœnsis (?)	–	–	73	25	521	61	1,085	316	53	–	350	5	435	168
R. setigera	–	–	–	–	4	–	–	–	–	–	–	–	–	–
R. stolterfothii	–	–	–	–	75	15	125	–	–	–	254	–	–	42
R. robusta	–	–	–	–	–	–	7	10	–	6	–	–	–	–
R. styliformis	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Skeletonema costatum	48	131	5,500	785	179	50,600	198	91	460	1,404	–	33	4,600	–
Schroderella schroderi	–	4	33	14	218	–	–	–	–	–	–	–	–	–
Thalassiosira gravida	420	275	786	570	279	175	–	24	–	–	–	–	–	34
T. subtilis	430	177	793	332	150	26	–	–	–	–	–	–	–	–
T. decipiens	–	–	–	82	–	19	–	–	–	–	–	–	–	–
Thalassiothrix nitzschioides	565	472	1,840	2,510	3,360	2,470	1,750	215	–	–	22	–	–	–
Phæocystis	–	13	13	32	–	–	3	130	–	–	15	–	–	–
Actinoptychus undulatus	–	–	6	–	–	–	–	–	–	–	–	–	–	–
Asterionella japonica	–	–	202	–	–	–	–	–	–	–	–	–	–	–
Cerataulina bergonii	–	–	3	–	–	–	–	–	–	–	–	–	–	–
Lauderia borealis	–	–	106	416	1,305	304	382	215	–	–	–	–	–	–
Navicula membranacea	–	–	3	3	29	–	7	–	–	–	96	–	–	75
Stephanopyxis palmeriana	–	–	30	–	108	11	30	–	–	–	–	–	–	–
Streptotheca thamensis	–	–	7	–	–	–	–	–	–	–	–	–	–	–
Leptocylindrus danicus	–	–	–	39	208	–	23	–	–	–	–	–	–	–
Navicula sp.	–	–	–	3	–	–	–	–	–	–	–	–	–	–
Noctiluca	–	–	–	7	–	–	–	–	–	–	–	–	–	–
Nitzschia closterium	–	–	–	–	–	8	3	–	–	–	–	–	–	–
Ceratium furca	–	5	10	3	–	–	–	–	–	6	–	–	–	–
C. fusus	11	7	–	21	33	38	7	48	42	608	37	125	241	66
Peridinium conicum	6	2	–	–	–	–	–	–	–	–	–	–	–	–
P. depressum	–	4	–	–	–	–	–	–	–	–	–	–	–	–
P. ovatum	–	5	6	18	–	–	–	–	–	–	–	–	–	–
Gymnodinium lunula	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Prorocentrum micans	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dinophysis sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Number of Cells per Litre.

June.			July.				August.				Sept.		October.			Nov.	Dec.	Jan.
4	11	18	3	9	19	27	7	15	24	31	11	21	2	18	31	14	10	1.'35
–	–	7	–	–	–	–	–	40	–	–	–	–	–	–	–	–	59	43
–	–	7	–	–	–	–	–	–	3	–	–	–	–	6	–	6	30	10
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	140	68	–	–	–	5	790	400	210	95	34	–	–
–	–	–	–	–	–	–	–	20	80	54	715	8,800	1,715	167	33	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	6	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	70	21	–	–	–	–	–	–	–	12	330	1,560	340	25	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	8,300	3,445	81	–	–	11	–
–	–	–	–	–	–	–	–	–	–	–	–	14,300	180	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	33	–	–	–	–	–	–	40	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	2,330	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	270	80	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	80	–	–	–	–	–
–	–	7	–	–	–	–	–	4	–	12	–	–	–	–	–	17	45	76
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15	–
–	–	–	–	–	–	–	–	–	–	–	–	6	5	–	–	–	–	–
279	–	147	–	–	–	–	20	–	–	–	–	–	–	68	–	–	–	–
–	–	–	–	–	–	–	–	8	–	6	10	–	–	6	–	–	–	–
104	98	7	1,790	243	350	640	116	196	21	54	72	–	50	155	–	–	–	–
–	–	–	–	9	–	–	–	–	–	6	–	–	–	–	–	6	22	30
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	– W	–	310	–	–	–	–
–	–	–	–	–	–	–	–	224	342	–	256	70	–	155	–	268	540	95
40	10,350	3,810	18	72	55	230	44	20	49	126	–	–	5	–	6	23	4	–
–	–	7	–	9	44	10	64	8	7	–	–	6	15	6	6	–	–	–
2,055	–	–	71	–	–	–	28	8	11	–	–	–	–	31	6	–	–	–
392	35	98	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	4	–	3	–	5	–	10	–	–	–	–	–
48	–	–	850	–	415	1,560	288	768	–	–	93	40	215	4,100	610	279	107	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	–	–	–
–	–	7	–	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–
–	–	21	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	66
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	21	–	54	98	30	–	–	14	6	–	–	–	204	–	188	244	16
–	–	–	–	–	–	–	–	–	–	–	–	–	–	12	–	–	–	–
–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	6	–	–	–
–	–	–	–	–	–	50	48	–	–	–	–	290	115	–	6	–	–	–
–	–	–	35	–	–	–	–	–	–	–	..	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–
–	–	–	940	243	490	280	–	4	–	6	–	–	20	43	–	–	–	
–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	6	–	–	65	43	6	159	4	36
–	56	84	257	72	–	–	–	–	–	–	–	–	485	87	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
263	28	42	27	27	11	70	100	12	31	6	–	–	–	–	–	–	7	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8	–	14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–	–	–	–	18	–	10	–	–	–	6	–	–	–	–	–	–	–	–
–	–	–	–	9	–	10	–	–	–	–	–	–	–	–	–	–	–	–

production took place from surface down to 45 metres. If the quantity of light over the 24 hours had been a ninth of that experienced, then the production would have been that taking place below about 16 metres in the experiments.

The total production between surface and bottom in summer and winter is thus roughly proportional to the areas enclosed by the whole curve and by that part of it which lies below 16 metres. In this case the effect of reducing the light to 1/9th would be to reduce the production of vegetation to 43%. In December–January the temperature is some 4° C. colder than in July; if this is taken into consideration (Matthai, 1904) it puts the winter rate of production per 24-hour period at about one-quarter the summer rate.

This calculation of relative magnitudes is not of general application, other species of diatoms may have different light requirements for growth and their compensation points may lie at different levels (Nielsen, in press). Moreover, diatoms are not usually distributed evenly between surface and bottom in nature.

The Plant Population.

The species and their numbers per litre in the water between surface and the 45-metre level are shown in Table I. These counts were made by the following procedure. A small quantity of the catch was placed on a slide and covered with a glass slip, the depth of the cell so formed being 1·75 mm. The numbers in the field of a microscope were counted after the diatoms had settled, the slide moved and the numbers in a new field counted. This was repeated in all five times, after which the slide was cleaned and refilled with a further portion of the catch. In this way the plants seen in 50 fields of the microscope, and in 0·194 c.c. of the catch —usually from about one-fifth of a litre of sea-water—were examined and counted. An analysis of several counts carried out in this manner was kindly made for us by Mr. G. M. Spooner and showed the values to have a satisfactory order of accuracy. In this way a record has been obtained throughout the year of the diatoms and peridinians in the water column at L4. The net has 200 meshes to the square inch, and when wet the open spaces, roughly rectangular in shape, average $41 \times 52\mu$ in a new net.* *It lets through a proportion of the smaller organisms.* For this reason the record gives minimal values, particularly when very small diatoms are at all abundant, and in the summer when diatoms are few and much of the plant life might consist of small cells which pass through the net. Water samples were examined by one of us in July and August, by sedimenting and examining the sediment from below, by centrifuging and by making a fine precipitate to carry down small organisms with it and examining this after centrifuging. It appeared that the greater bulk of the chlorophyllaceous matter was in organisms such as were caught in the net.

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* Henson gives an average of $48{\cdot}7\,\mu$ for new and $30{\cdot}6\,\mu$ for much used material.

With plants of such greatly differing size no exact relation would be expected between the number of diatoms per cubic metre and the quantity of plant pigments in them. However, if allowance is made for the size of only three species, whose cell contents were small and each of which was found in preponderating quantity at times between January and September, a clear correlation is seen. Figure 7 shows that the arbitrary "units of plant pigments" found per cubic metre of water and the number of plant cells per cubic metre, weighted so that 20 cells of *Skeletonema costatum* or 3 cells of *Rhizosolenia alata* or $3\frac{1}{2}$ cells of *R. shrubsolei* are counted as one "diatom of average cell contents." In September when several species of Chætoceros appear in quantity further weighting would be necessary to continue the correlation.

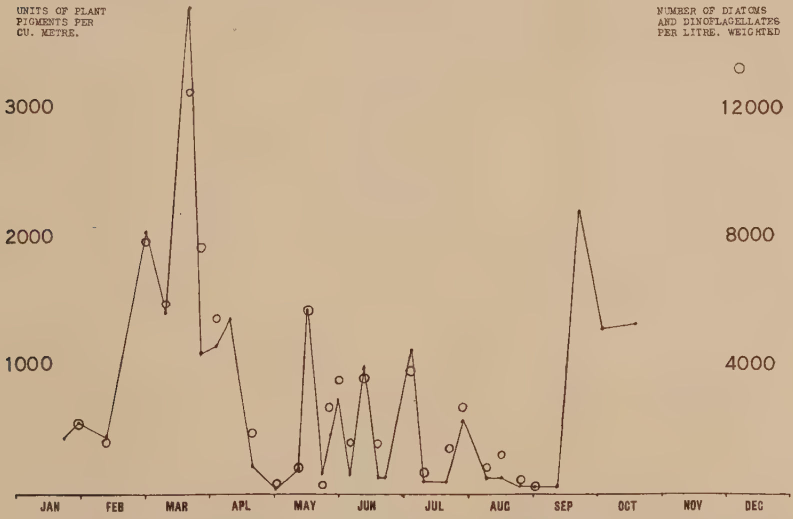

Fig. 7.—The points on the curve show the units of plant pigments per cubic metre in the water column between surface and 45 metres at Station L4. The circles show the total number of diatoms + dinoflagellates per cubic metre, the observed number of three species of diatoms being weighted.

During the early part of the year hauls rich in diatoms were obtained and it was possible to free them from most of the animal organisms present by filtration through bolting silk having 50 meshes to the linear inch. These opportunities were taken to find the relation between the phosphorus content of the diatoms and their content of plant pigments with the following results.

	Mg. P found.		Units of plant pigment found	Mg. P per 1000 units of plant pigment after arbitrary allowance for P in animals, etc.
January 1/34				
Almost pure phytoplankton . .	0·039			
	0·037			
	0·039			
		·039	286	$0{\cdot}13_5$
February 7/34.				
About 30% of bulk was animal plankton	0·611			
	0·676			
		·643	4000	0·13
February 20/34				
About 20% fæcal pellets . . .	·189			
	·185			
		·187	3400	$0{\cdot}05_5$
April 3/34				
Nearly all diatoms . . .	0·244			
	0·243			
	0·275			
		·252	2400	0·10
May 15/34				
About 20% animals . . .	(0·304)			
	0·465			
		·46	5200	0·07

In both 1933 and 1934 the same type of seasonal variation occurred, as shown in Figure 8. In 1933 growth commenced a little later, as there was less sunshine in February, but continued more rapidly, there being more sunshine in March. Then the population decreased more suddenly and completely at the beginning of April, although there was more sunshine during the first half of April than in 1934. During the summer the outbursts were more intense than in 1934, consisting mainly of *Rhizosolenia alata* in May and of *R. stolterfothii* and *Guinardia flaccida* in June, whereas in 1934 the May outburst was mainly composed of *R. shrubsolei*, the June outburst of *R. alata* and the outburst at the beginning of July of *Guinardia flaccida.*

> It was possible to determine the pigment content of *R. alata* in both years. In 1933 one unit of plant pigments was contained in 7,300 cells while in 1934 the same quantity of plant pigments was contained in 11,300 cells, suggesting that the cells were rather smaller in the latter year.

The autumn outbursts commenced in September. In 1933 it was composed mainly of *R. styliformis* and *Biddulphia sinensis*, the population increasing more gradually than in 1934, attaining nearly twice the density and continuing until December. The autumn of 1933 was notable for many sunny days while in 1934 dull days prevailed in November and early December. In 1934 the outburst was composed almost entirely of several species of Chætoceros.

Although the same type of seasonal changes took place during the two years, it is clear from Figure 8 that the supply of vegetable food for animals was very different.

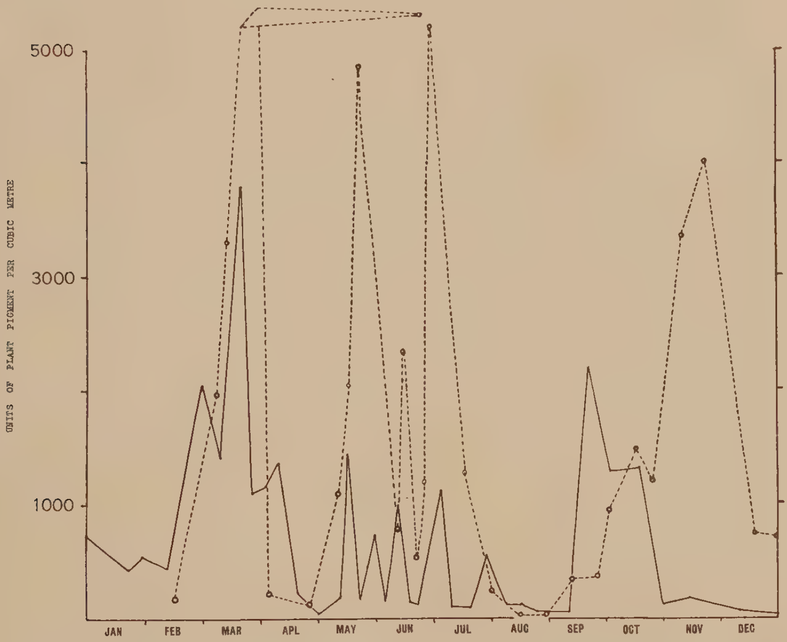

Fig. 8.—The points on the full-line curve show the units of plant pigments per cubic metre during 1934 and the circles on the dotted curve during 1933, at Station L4 between surface and 45 metres.

Furthermore, it seems reasonable to conclude that with the larger average breeding stock of diatoms in 1933, the production of vegetation was greater than in 1934, and their nutrient salt requirements greater also. This appears to have been the case since the difference between the maximum phosphate content of the water column found at the beginning of the year and the minimum found in the summer amounted in 1933 to some 17 mg. and in 1934 to 12 mg. phosphorus per cubic metre.

The Animal Plankton.

The plankton animals in an aliquot part of each catch were counted. The total animals and the proportion of the more important organisms are given in Figure 9, which shows a seasonal increase from a low winter minimum to a maximum in September, with considerable fluctuations during the summer months. The composition of the copepod population is given in Figure 10. It shows that the late summer production of copepods is largely made up of the small species, Oithona, and of " small copepods " (mostly Pseudocalanus), while in May the much larger species, Temora, was abundant.

The counts were made in the following manner. From 100 c.c. portion of the catch (derived from 70 to 150 litres of sea), the larger organisms were picked out—all medusæ, Calanus, adult Temora, Centropàges, Sagitta, decapod larvæ and other large organisms together with most adult Pseudocalanus. All organisms and fæcal pellets in a 10 c.c. portion were then counted under the microscope. When counting, the first two of three copepodite stages of each species of copepod were lumped together as " small copepods " to give some index of relation of early to late stages.

To obtain a true picture of the quantity of animal plankton it is necessary to make some estimate of its volume, which requires size measurements of all the animals involved. It was thought that the phosphorus content of the zooplankton would give an even better index of the quantity of animal matter than any volume measurements.

An attempt has been made to compute the volume of the catches. The average volumes for the different organisms given by Lohmann (1908, Table XI) have been used, while volumes for Sagitta and Calanus have been calculated from observations given by Gunther (1934). The computed volumes of some of the total catches so produced are given in Figure 11. This shows that, on the whole, late summer quantities are somewhat less than those for May, as was indicated by the composition of the copepods. In this same figure are given the calculated amounts of animal phosphorus in each of the catches whose computed volumes are shown. The agreement between the two curves is good, with the exception of two anomalies on May 23rd and September 11th. The agreement in the second half of the year is not so good as in the first half. The computed volumes for the animals then should possibly be slightly lower since allowance could not be made for the smaller size of the same species of plankton animals in summer than in spring.

The general agreement between the two curves is however sufficient to show that the phosphorus estimations usually gave a good approximation for the total quantity of animal matter present in any one catch.

Although a considerable population of animals was supported in late summer they did not reach in actual animal matter the high spring values. In this respect our results are unlike Lohmann's, who found a greater production both of animals and plants in the late summer months. It should however be noted that Lohmann's late summer data are supplied for the year previous to his spring figures. Examination of his table on

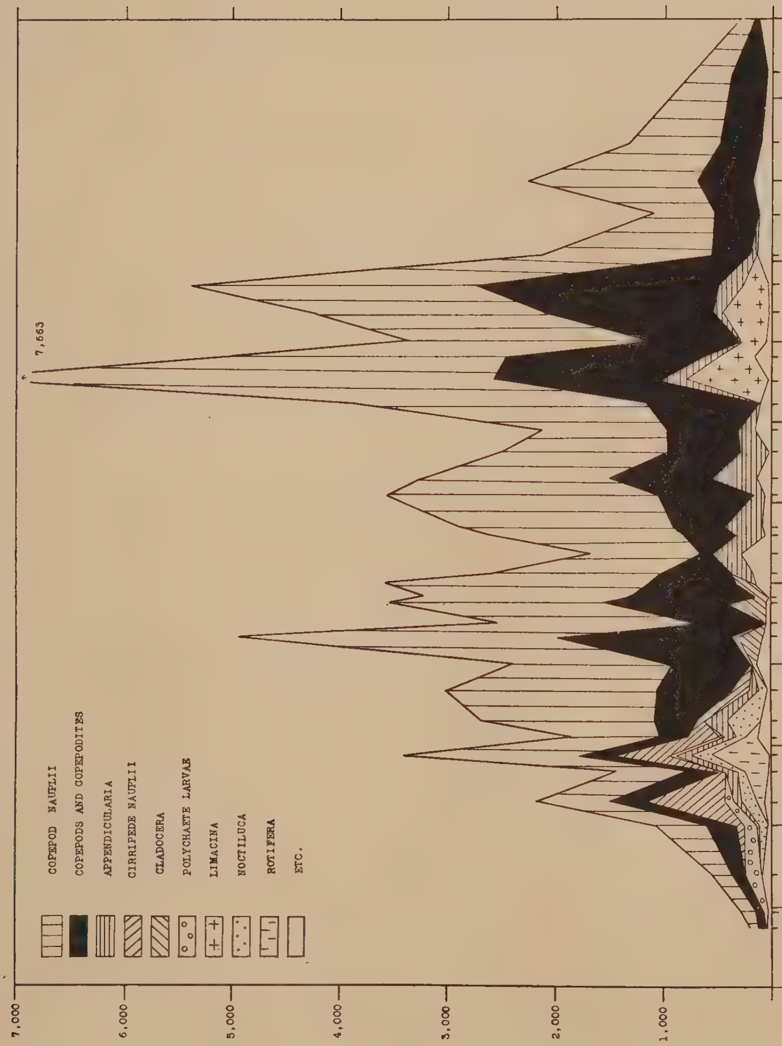

Fig. 9.—Diagram showing the total number and composition of the animals caught per cubic metre of water at Station L4 between surface and 45 metres during 1934.

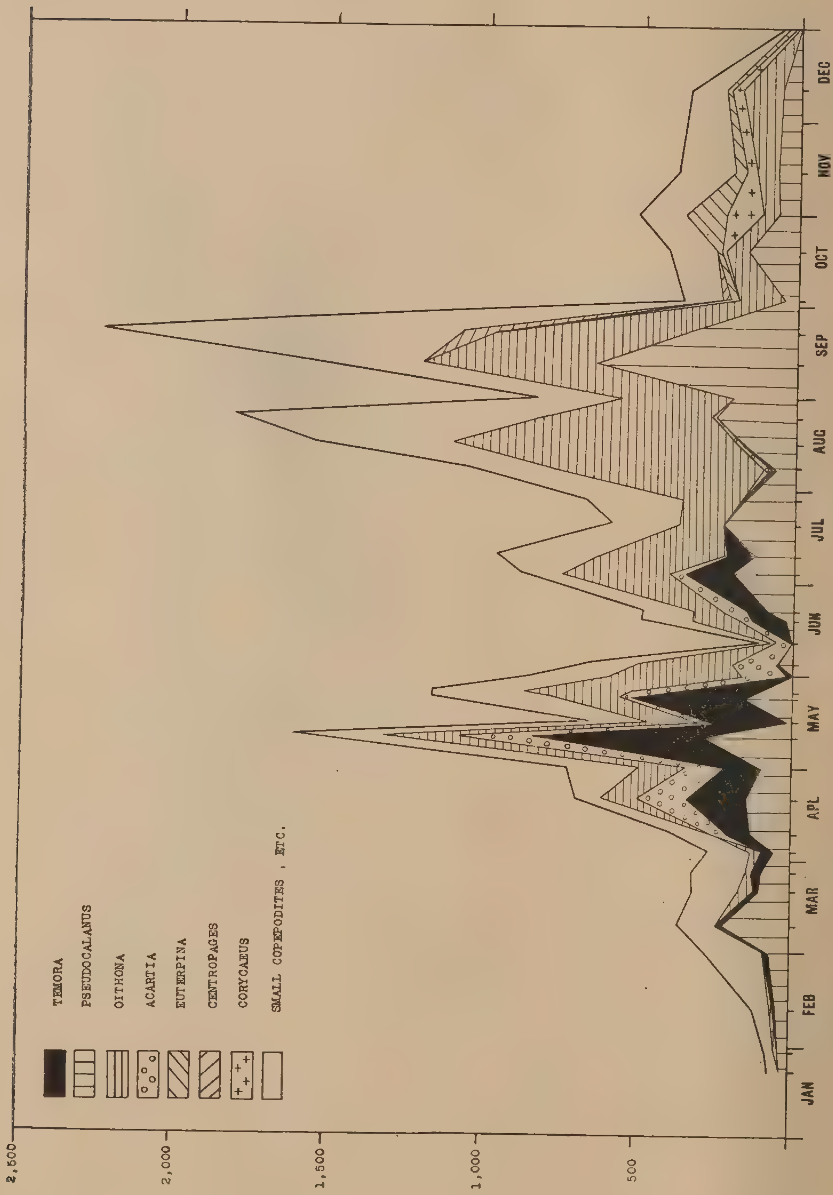

FIG. 10.—Diagram showing copepods caught per cubic metre of water at Station L4 between surface and 45 metres during 1934.

page 345 shows that while in August, 1905, the volume of plants was 109 c.mm. and of animals 46 c.mm. yet in 1906 it was only 51 and 32 respectively. It seems likely that by combining the two years as one consecutive calendar year a false impression has been produced. Our results for 1933 and 1934 show that the plant production in 1933 was throughout greater on the whole than in 1934 and it may well be that the year 1905 at Kiel was one of greater production than 1906.

The fæcal pellets found in the catches were too large to have been produced by copepod nauplii, and indeed many may have been produced by animals which were not caught in our net because they remained on the bottom during the day or because they were swift enough to escape it.

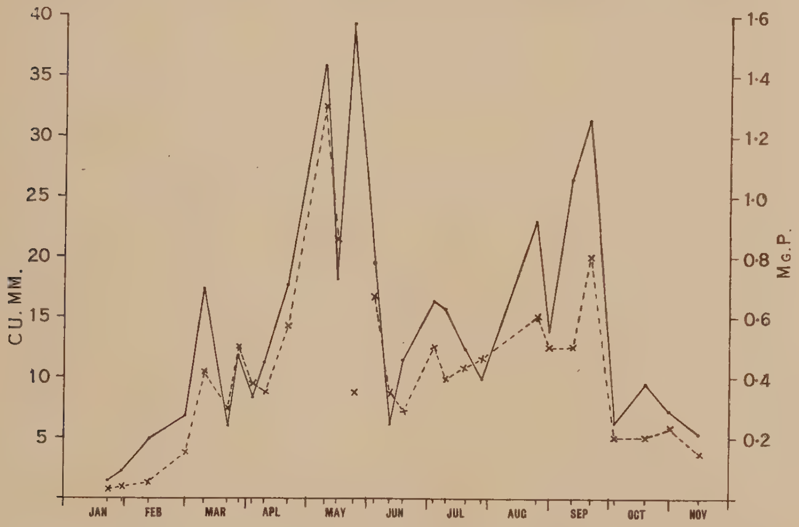

Fig. 11.—Points on full-line curve show the estimated volume and crosses (on dotted curve) show estimated phosphorus content of animals caught per cubic metre of water.

In Figure 12 the numbers of fæcal pellets per copepod and copepodite are plotted against the plant population. This shows that the numbers of fæcal pellets bear a distinct relation to the amount of plant food available and seems to indicate that the amount of plant food eaten depends rather on the amount of food available than on the dietary requirements of the animals. It was noticeable that in spring when the numbers of plants were very high in relation to the number of animals the many fæcal pellets present were distinctly green, suggesting that a large part of the plant matter had been passed through undigested.

During the months March, April and May most of the Temora and the Cirripede larvæ had their alimentary canals packed with food. This was in marked contrast to the few animals containing food in the late summer.

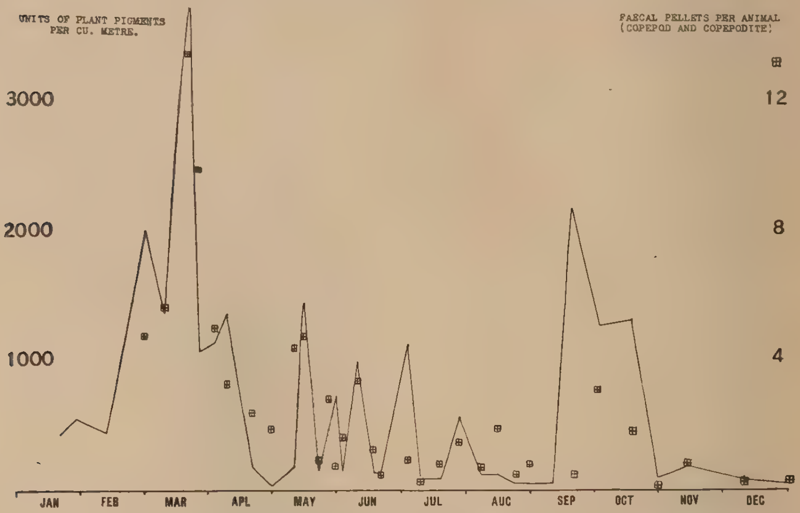

FIG. 12.—Points on curve show the units of plant pigment per cubic metre, and squares show the number of faecal pellets per copepod + copepodite in the water between surface and 45 metres at Station L4.

It suggests that certain species are more voracious than others. Marshall (1924, p. 478) has also observed that "Temora appears to be more voracious." It may not be without significance that the first decrease in plant pigment in March corresponded with the period of abundance of cirripede larvæ, while the heavy decrease in April and the beginning of May took place at the time when Temora were most abundant.

A greater total production of plants and animals was found in the waters of Kiel Bay than at the Station L4. The monthly average numbers of animals in 100 litres of water were as follows :—

	L4, Plymouth.		Kiel Bay.	
January	239	1934	3,700	1906
February	545		4,700	
March	2,024		6,000	
April	2,518		5,800	
May	3,365		28,000	
June	2,440		7,400	
July	2,852		37,000	
August	4,963		7,600	
			19,000	1905
September	4,818		24,000	
October	1,839		24,000	
November	1,338		13,000	
December	736		5,700	
	27,677		190,000	

The greater numbers at Kiel are accounted for largely by Oithona and its nauplii, and by Rotifers in May and July ; as a result the computed volumes of the animals are not so widely different between the two localities, except in the winter months when animal life was very much more abundant at Kiel than at Plymouth.

THE SPRING CONDITIONS.

The species which, on account of their numbers or their size, make up the bulk of the spring plant growth, were present in the water in January and February in significant quantity, with the exception of *Lauderia borealis*.

The diatom population did not attain the density found in the previous year, and in neither year did it attain anything approaching the density attained in some other places, such as Kiel Bay, Loch Striven or Oslo Fiord.

In 1933 the quantity of vegetation produced during the spring flowering was calculated from the phosphate taken from the water by the diatoms during the period of spring growth. This exceeded by many times the quantity of diatoms observed in the water. This calculation of magnitudes, in conjunction with the presence of many fæcal pellets of herbivorous animals, green with diatom remains, led to the conclusion that the crop was being extensively grazed and disappeared because it was eaten (Harvey, 1934). Again in 1934 the estimated production of diatoms during the period of the spring outburst exceeded by many times the population found present on any day when samples were taken. Neither diatoms which were obviously dead nor empty frustules were found in any quantity. The L4 area has a clean gravelly bottom well scoured by tidal streaming. The diatoms disappear, unless there may be a suspension of diatoms close to the bottom which we have failed to find.* A relation between the numbers of animals and of plants was found, an increase in animals being accompanied by a decrease in diatom population (Figure 13). The number of fæcal pellets green with diatom remains is also of interest. On March 20th, when the diatoms exceeded the animals to the greatest extent, the greatest number of pellets were found. This suggests that during this period when the diatoms are most abundant in the water the animals eat far in excess of their needs.

It is of interest to consider surveys of other areas where the observations are such that they bear upon this question. Boysen Jensen (1915) while investigating the deposition of organic detritus in Danish waters calculated the monthly production of phytoplankton. He made vertical hauls with a net from surface to bottom to estimate the phytoplankton population per unit area of the sea, and, regarding this population as a variable capital fund which daily yields a certain percentage of its amount, calculated this yield for each month. He used values for the rate of reproduction of the organisms based on Karsten's and on Gran's observations of diatom growth rate. From the magnitude of this calculated yield or production, which must be finally either deposited on the bottom or consumed by other animals, he concluded that " only a limited proportion of the plankton production is deposited on the bottom ; how large a proportion this may be it is impossible to say."

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* During and after the spring outburst of 1935, samples of water were obtained from a few inches above the bottom by means of a hose and pump. The observations showed no material accumulation of diatoms in the bottom layer which was not traversed by the measuring net.

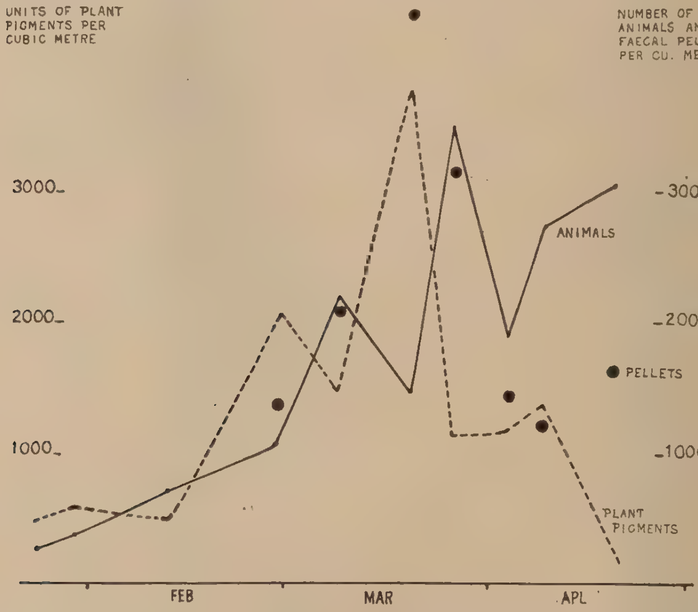

FIG. 13.—Points on dotted curve show the units of plant pigments, on full-line curve the total number of animals and the black circles show the total number of faecal pellets caught per cubic metre of water at Station L4 between surface and 45 metres.

In Loch Striven Marshall and Orr (1927, 1930) have observed the diatom population at various depths between surface and bottom at intervals throughout the spring growth, which consisted almost exclusively of *Skeletonema costatum*. These attained a population density many times greater than diatoms in the open sea at L4, even after allowing for their small size, and " disappeared " while there was still much available phosphate remaining in the water. Usually less than a month intervenes between the beginning of their rapid rise in numbers and their relatively complete disappearance, whereas at L4 the spring outburst lasted six weeks to two months in 1933 and 1934. Their distribution in Loch Striven varied in different years. In 1928 a dense growth took place in the upper layers, but the diatoms were never found in quantity near the bottom. It seems probable that they were eaten while sinking and before reaching the bottom. In 1926 (Figure 14) the dense growth extended downwards and great numbers were found in the bottom water a few days before their sudden disappearance from all depths. This suggests that the Skeletonema was not all eaten, but that a part settled to the bottom. The sudden "disappearance" of the diatoms from the upper layers between April 13 and 20 is remarkable unless they were eaten, because during this period there was a significant quantity of phosphate utilised, suggesting that active growth was taking place up to the end. Moreover, there was a recrudescence of the same species about a week later, and, furthermore, during the interval polychæte larvæ were abundant.

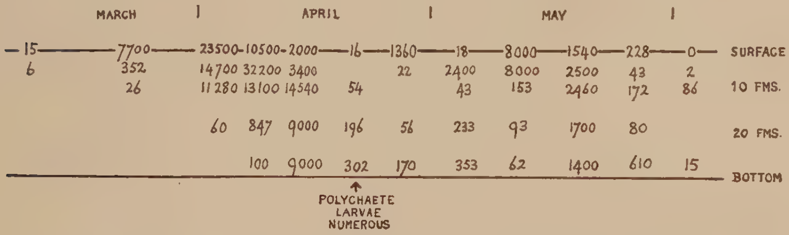

FIG. 14.—Diagram showing the number of chains of *Skeletonema costatum* in 20 c.c. at Clapochlar, Loch Striven. (Data supplied by Miss S. M. Marshall.)

Annual bands of humus are found in the mud of the Clyde Sea area, which Moore has shown to be laid down each spring and formed from the organic matter (in fæcal pellets composed of partly digested diatoms with some dead diatoms), which is deposited during and after each spring outburst. In 1930 he suspended pots at depths of 18 metres and 68 metres in Loch Striven (Table II).

During the period of the spring outburst, which reached a maximum on March 28th, diatoms were deposited in the upper pot in great numbers from March 4th to about March 26th after which date the numbers of diatoms decreased and great numbers of fæcal pellets were deposited. In the bottom pot diatoms did not start to be deposited until about March 26th. Many were deposited during the week ending April 2nd (3,800 cells per sq. cm.).

TABLE II.

From Data supplied by H. B. Moore.

	Pot at 18 m. No. of Skeletonema cells per cm.^{2} per week.	Pot at 68 m. No. of Skeletonema cells per cm.^{2} per week.
1930		
March 4–11	11,500	
11–18	1,040,000 almost pure diatoms	
18–26	669,000	No diatoms, some green fæcal pellets.
26–April 2	84,000 with some green fæcal pellets	3,800 with many pellets.
April 2–23	Some diatoms with very many fæcal pellets	Some diatoms with very many fæcal pellets.
Total No. of Skeletonema cells deposited March 4—April 23	Less than 2,500,000	Considerably less than 2,000,000 probably less than 500,000.

After which great numbers of fæcal pellets fell and made counting the diatoms, which appeared to be decreasing, impossible.

If we take the estimate of the maximum number of diatoms deposited from the column of water 6,800 cm. deep, then these diatoms if evenly distributed throughout the column of water would amount to $\frac{2,000,000}{6,800} =$ 295 per c.c. or 500 chains per 20 c.c. During the maximum in 1926 the population averaged some 9,000 chains per c.c.

The evidence indicates that only a small part of the spring outburst of diatoms is deposited on the bottom, without passing through the animals.

During the 1926 spring outburst in Loch Striven a similar quantity of dissolved phosphate was utilised by the plants below each square metre, as is utilised by the spring growth of plants at the Plymouth Station, L4. It follows that a similar quantity of vegetation was produced in both areas, although in Loch Striven it reached a remarkable density in the upper layers (over 16 million cells of Skeletonema per litre at 5 fathoms), and the average density of vegetation in the whole column of water from surface to bottom on April 7th exceeded by several times the maximum found at L4. A simple explanation of this difference would be that the herbivorous animals are fewer at the beginning of the outburst than at L4 and allow the population to build up more rapidly. As yet we have no knowledge of their relative numbers in Loch Striven. Conditions common to this and similar areas may influence their attaining a denser plant population than the open sea.

The water contained more dissolved phosphate at the beginning of the 1926 outburst in Loch Striven than it does at L4 (1933, 1934), and growth is more rapid the higher the concentration of nutrient salts—at least for one species of diatom (Harvey, 1933). In Loch Striven the turbulence set up in the water by wave motion is less than in the open sea and there is no turbulence set up by tidal streaming or currents. Hence diatoms in the upper layers where light conditions are best for growth can better remain there, not being continuously moved to greater or lesser depths. Under these circumstances of optimum light a layer of dense population can be most rapidly formed, and having once formed the animals may avoid it* preferring to feed below it where the vegetation is ample but less dense and less likely to tangle about them. Thus a focus where plant growth is most rapid and grazing least intense would be formed, and persist until the animals having increased in numbers eat into it.

The evidence all seems to point to the spring growth of diatoms, both in the Plymouth L4 area and Loch Striven, being regulated by the intensity of grazing.

The Magnitude of the Spring Crop of Phytoplankton.

From the quantity of phosphate in the water which has been utilised, and the average phosphorus content of spring diatoms, the total production or crop of diatoms during the period may be calculated.

In the early part of 1934 the general hydrographic conditions and the fluctuating phosphate content of the water were unusual, and the data collected at L4 is not necessarily typical of a watermass which has occupied a coastal area of similar depth and illumination during the whole period. In order to calculate the crop it is necessary to assume that it had done so, the decrease in phosphate due to utilisation by diatoms being some 6 to 8 mg. P per cubic metre between the middle of February and the middle of April. The regularity with which a fall in phosphate has been observed over a number of years and its magnitude, suggests that this is a reasonable estimate. During the early part of the previous year 1933, this uncertainty is less. Between February 16th and March 28th the water at L4 lost some 6·75 mg. P per cubic metre due to its utilisation by diatoms.

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* The avoidance of thick phytoplankton by the animals has been suggested by Professor A. C. Hardy.

In order to arrive at an average value of the phosphorus content of the diatoms over the period of the spring flowering, the phosphorus content of the phytoplankton catches per cubic metre of water was calculated (Figure 15) on the basis of the three sets of analyses made during the period (*vide* p. 418). It shows that the average phosphorus content of the diatoms was roughly 0·14 mg. P per cubic metre. Their average content of plant pigments being 1,800 units, this gives an average ratio of 0·08 mg. P per 1000 units of plant pigment, or 4×10^6 diatoms "of average cell contents" (p. 417).

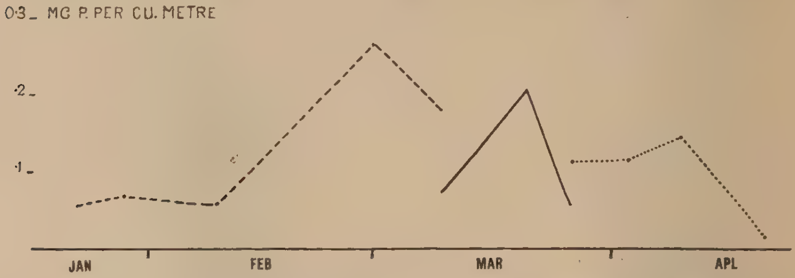

FIG. 15.—Pecked line shows phosphorus content of phytoplankton per cubic metre, calculated from ratio found on February 7. Full line from ratio found on March 20 and dotted line from ratio found on April 3.

It follows from this that the total production or crop during the spring flowering between the middle of February and the middle of April in 1934 was a quantity of diatoms containing some $\frac{6 \times 1000}{0{\cdot}08}$ or 75,000 to $\frac{8 \times 1000}{0{\cdot}08}$ or 100,000 units of plant pigments, and during the six weeks period between February 16th and March 28th, 1933, a quantity containing some 85,000 units of plant pigments.

It is clear that the validity of these calculations depends upon our having struck a fair average value relating phosphorus content to pigment content to number of diatoms. The value cannot legitimately be applied to mixtures of other species of diatoms, but it was thought, however, that the result of applying such calculation to Marshall and Orr's Loch Striven data for 1926 would be interesting although grossly speculative.

The decrease in phosphate since March 23rd in a column of water, 1 sq. metre cross section, extending from surface to bottom, was calculated for each day on which samples were taken. The population of Skeletonema on each day was also calculated The number of Skeletonema cells produced since March 23rd on each date was arrived at in the following manner. We had found at L4 that 20 cells of *Skeletonema costatum* contained roughly the same quantity of plant pigments as one diatom of average cell contents

(p. 417) and 4×10^6 of these contained 0·08 mg.P. We are indebted to Miss Marshall for measuring cells of Skeletonema caught at L4 on March 26th, 1934, and in Loch Striven during the spring of 1926 with the result that 28 cells from Loch Striven had the same volume as 20 from L4. From this the assumption is made that 0·08 mg.P was contained in $28 \times 4 \times 10^6$ Skeletonema in Loch Striven. The phosphate utilised since March 23rd being known, the production of Skeletonema was calculated. These values are shown as circles in Figure 16. Movement of the water mass had taken place, particularly between March 23rd and April 7th, shown by change in salinity and by the irregular change in phosphate content. On account of this and the gross assumptions used in the calculation, the dotted curve is a conjecture.

The Rate of Diatom Growth during the Spring Flowering.

In order to make a speculative estimate of the rate of growth the assumption has again to be made that the quantities of diatoms actually found at L4 on the various dates are representative of the population in the watermass which occupied the area in April.

During the two months in 1934 the average population of diatoms found at L4 contained some 1,800 units of plant pigment, and to have produced a total crop containing 75,000 units must have divided about 40 times in the 60 days—an average of once every 36 hours. To have produced a total crop containing 100,000 units the average rate works out at once every 26 hours.

During the 40 days between February 16th and March 28th, 1933, the average population contained some 2,500 units of plant pigments, and to have produced a total crop containing 85,000 units, must have divided about 34 times in 40 days—an average of once every 28 hours. These estimates are in fair agreement. On the other hand their magnitude, but not their agreement, depends upon our having assessed the very variable ratio of phosphorus to plant pigment in the diatoms correctly. Furthermore some of the phytoplankton undoubtedly passed through the measuring net, which makes the estimated rates too high.

These estimates suggest that the diatoms divided on the average about once every 36 hours. This takes place for the most part in March, when the average daily illumination is only about one-third of its summer value and any material photosynthesis over a 24-hour period is not likely to take place below 25 metres, or half-way to the bottom, even in the transparent water at L4. As the diatoms are evenly distributed between surface and bottom, this suggests that the diatoms above 25 metres divide, on the average, once in less than 18 hours.

This speculative estimate gives a rate—a maximum rate—which is strikingly high. However, spring diatoms do reproduce very rapidly at times. In 1922 Gran filled flasks with natural sea-water rich in diatoms and immersed them in the sea at a depth of 1 metre for three days between

March 8th and 11th, when the numbers rose from 17,220 to 170,340 per litre showing that they divided on the average once in rather less than 24 hours. In a similar experiment one of the included diatoms, *Biddulphia aurita*, rose in numbers from 280 to 30,040 per litre in flasks immersed at 2 metres and to 23,000 at 5 metres during three days, March 22nd–25th, 1916, dividing on the average once every 10 hours. The temperature of the Norwegian sea is about 5° C. colder in March than that of the English Channel.

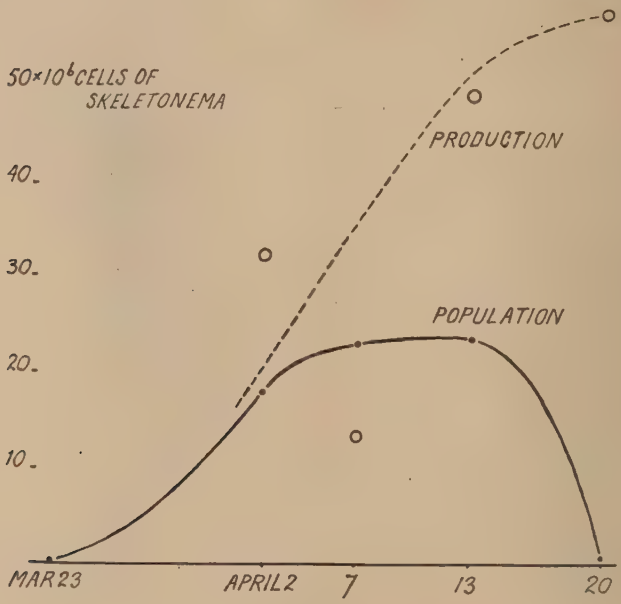

FIG. 16.

In Loch Striven during the eleven days between March 23rd and April 2nd, 1926, the population of diatoms below each square metre increased from some 9×10^9 or less to some 180×10^9 individual cells. This corresponds to an average of one division in about 48 hours, or in less if allowance is made for diatoms eaten during the period. This minimum rate of one division in 48 hours corresponds with our calculated maximum rate of one division in 36 hours; both being average rates for the entire water column.

THE FATE OF THE SPRING CROP.

Our estimate of the production, which is in the order of 340,000 diatoms of average size per litre, exceeds by many times the population found to be present on any day when samples were taken during the spring outburst. Neither diatoms which were obviously dead, nor empty frustules, have been found in any quantity. The L4 area has a clean gravelly bottom well scoured by tidal streaming, and, unlike Loch Striven, there is no annual deposition of mud. The crop disappears; we have failed to find a suspension of dead diatoms in the water close to the bottom.

It is of interest to calculate how much vegetable matter plankton animals eat during the period of the spring outburst, on the supposition that they alone eat almost the whole estimated crop, no account being taken of those eaten by the bottom fauna and larger animals. Raben's analyses of plankton show that the N to C ratio is variable, but on the average similar in animal plankton and diatoms, Cooper's that the P to N ratio is similar. Hence for a rough approximation it is assumed that quantities of living animal and plant plankton containing the same quantity of phosphorus, contain about the same weight of organic matter. The diatom crop per $m.^3$ contains some 7 mg. P—an average daily production of diatoms containing 0·11 mg. P—and the animal plankton present on any one day, between the middle of February and the middle of April from our estimates contained on the average some 0·29 mg. P or two and a half times that of the average daily plant production. The deduction that rather less than a half of the herbivores own weight is on the average eaten daily, as a maximum estimate, lies within the bounds of possibility. The magnitude of the animals feeding rate if they regulate the diatom population can also be estimated in other terms. From Figure 1 it appears that the animals eat down the daily production of diatoms from a breeding stock containing 1/10th of their number of units of plant pigments, or 400 times their number of diatoms "of average cell contents," dividing about once every 36 hours. That is, each animal eats some 270 diatoms of average size daily. Again on March 20th, if the animal plankton was just keeping the diatom population from increasing, then animals containing 0·3 mg. P were eating daily diatoms containing $\frac{24}{36} \times 0{\cdot}208$ mg. P or roughly half their own weight, each animal on the average eating $\frac{12{,}697{,}000}{14{,}470} \times \frac{24}{36}$ or 570 plant cells.

The copepod *Eurytemora hirundoides* has been observed by Lucas (private communication) to eat as many as 5,000 cells of the very small diatom *Nitzschia closterium* hourly, or 120,000 per day. From Atkins' observation (1923) these would contain 0·000056 mg. P, which is contained in some 2,800 diatoms of average size.

The extent of the part played by the bottom fauna is unknown. If each average square metre of the bottom contains filter feeding organisms comparable in activity to 3 or 4 common mussels, they will only filter the diatoms from some $\frac{1}{4}$ m.^{3} of water every 24 hours, that is 1/200th of the water column. From this consideration it seems unlikely that they play a material part in determining the diatom population of the water column from day to day. On the other hand it is not improbable that many diatoms at times sink and remain in the water close to the bottom until they are ingested by the bottom fauna.

These considerations suggest that only a part—probably even a small part—of the spring crop is converted directly into animal tissue, the remainder being present in the form of fæcal pellets, the detritus formed from them, and, in some areas, of dead diatoms close to the bottom. In some areas a rich bottom fauna is supported by this remainder.

The possible fate of that part of the spring crop which is not converted into animal tissue may be traced a little further. Analyses of fæcal pellets, green with diatom remains, showed that they were poor in phosphorus and suggest that much of the phosphoproteins and phospholipins dissolve into the sea when diatoms are eaten but only partially digested by copepods. A period of three to four months intervenes between the disappearance of the spring crop and the reappearance of phosphate in the water ; after the spring outburst the phosphate in the water continues to decrease—the rate at which it is used by phytoplankton exceeding the rate at which it is reformed—until some time in July or August.

These present researches have shown that a very considerable accumulation of dead diatoms would have to break down in order to provide the phosphate which reappears in the late summer, and as we do not find any such accumulation, the phosphate is not apparently reformed directly from dead diatoms. If the phosphate were reformed directly from animal tissue we should expect a noticeable mortality of animals shortly before the reformation at the end of summer, but no such mortality is known to take place. Much of the phosphorus compounds may dissolve out of broken diatoms when they are eaten but only partially digested by zooplankton at the times of diatom maxima and remain in solution during the interval until finally broken down into phosphate by bacterial action. These vegetable phosphorus compounds are stable and only break down slowly into phosphate. If solution of the contents of the broken and partially digested cells into the water is the fate of any considerable part of the spring crop we should expect more dissolved organic matter, particularly organic phosphorus compounds, in the water in May than in the winter months. Analytical methods are only now becoming sufficiently developed to investigate this.

THE SUMMER POPULATION.

Early in April many of the species of diatoms which are plentiful in March cease to be represented, except by occasional individuals, and do not appear again in the catches before the autumn or even later. The Baccillaria, Biddulphia and Coscinodiscus are cases in point. Relatively few Chætoceros occurred during the summer although plentiful in March and making up most of the September catches. These spring-autumn diatoms proliferate when the water is coldest and again when it is quite warm in autumn; at both seasons the length of day is roughly 12 hours.

The summer population was composed of species which were well represented throughout the year, in the case of *Guinardia flaccida*, *Rhizosolenia alata*, *shrubsolei*, *stolterfothii* and *Navicula membranacea* reaching a greater concentration in the summer than at other times.

At the beginning of the period *Skeletonema costatum*, a diatom typical of springtime, was found in varying abundance until the end of May. Only a fraction of this minute species will be retained by the silk net, and owing to its loss our values for the plant population are likely to be too low during April and May.

On May 10th a dense animal population was encountered with many green fæcal pellets, in water with few diatoms. It is hence probable that an outburst of diatoms, which we missed, had taken place just previously and been eaten down.

The outbursts of *Rhizoselenia shrubsolei* on May 15th and 30th and of *R. stolterfothii* and Guinardia on July 27th occurred at times when the animal population was relatively low. It was thought that these summer outbursts were of limited area and took place where the intensity of grazing allowed. The 1933 survey suggested that in June " the zooplankton may have occurred in swarms, accounting for the uneven distribution of diatoms." On May 25th, 1934, a series of observations were made at varying distances off shore and showed a variable plant population. On July 27th a number of observations were made in the vicinity of L4 and it was found that the water to the south and west contained few diatoms. The number of animals and units of plant pigment in the water at a position 2 miles to the south of L4 were ascertained and show more animals with fewer plants.

	At L4.	2 miles south of L4.
Units of plant pigments/m.^{3}	560	100
Animals/m.^{3}	21,290	32,690
Fæcal pellets/m.^{3}	9,070	1,200

On the other hand the outburst of Guinardia found on July 3rd was in water with relatively many animals, of which however the proportion of nauplii was very high.

During the greater part of August and the first week in September, 1934, the phytoplankton caught in the net at L4 was sparse. Examination of the water failed to show any material quantity of small vegetable organisms which would have passed through the net. There was on the other hand a considerable quantity of organic detritus in the water.

Meanwhile the zooplankton remained abundant. The number of fæcal pellets per animal remained low, and they were never tinted green with diatom remains (Figure 12). It is not unlikely that much of the zooplankton, normally herbivorous, was feeding on detritus with its associated protozoa and bacteria.

If we consider the plant population from day to day as the breeding stock or capital fund, the daily production of vegetation can have been very little during this period, even if the net was letting through its meshes as great a weight of small plant organisms as it was catching. However, it is possible that the breeding stock during the summer is augmented owing to the presence of " spores." In September, 1918, the plankton in a sample of sea-water was counted after separation by centrifuge and also determined by a culture method (Allen, 1919). By counting, the number of diatoms was found to be 12,200 per litre, and by the culture method 376,000. Amongst the diatoms were several large species which, as well as the small species, were found to be more numerous by the culture method. A sample of water collected in August was also examined by the culture method and found to contain 290,000 diatoms per litre. " To what extent the number found represents individual cells and to what extent it represents ' spores ' it is impossible to say definitely."

This classical experiment suggests the possibility that the L4 area is heavily seeded during the late summer, and perhaps capable of a rather considerable daily production of vegetation.

It seems clear from Figure 12 that the animals feed heavily when there is much food present, greatly in excess of their needs. From the data obtained during this survey we have no means of gauging the minimal food supply necessary. Concerning the magnitude of this there have been many estimates made (Pütter and others), perhaps the most suitable for our purpose being an investigation of the metabolic rate of the copepod *Calanus finmarchicus* (Marshall, Nicholls and Orr, 1935). This indicates that this animal, typical of the majority of zooplankton, requires less than 5% of its own weight daily of digestible vegetation. As a very rough approximation we conclude that the summer zooplankton per cubic metre containing an average of 0·6 mg. P will require daily, if two-thirds of them depend on vegetation, a quantity of phytoplankton containing 0·002 mg. P or 30 units of plant pigments or 120×10^3 diatoms of average size.

The daily production of this quantity of vegetation could reasonably be expected. It is a quarter of the average diatom population caught in the measuring net during this period.

If the sparse plant life in August, by means of normal binary fission provides a sufficiency of food, as is suggested by this rough calculation, then during the rest of the year a very considerable excess of vegetable foodstuff is produced.

This excess, the greater part of which seems to be eaten but only partially digested, is not necessarily unused. Some of it at least is converted into the protoplasm of flagellates on which in turn other animals feed. When a culture of diatoms dies a dense population of flagellates springs up; Marshall, Nicholls and Orr found minute flagellates in great numbers in Loch Striven immediately following two diatom maxima (Marshall, Nicholls and Orr, 1934).

However, even if this is taken into account, these observations indicate a great wastage of vegetable food by the plankton except during relatively short periods in the summer.

In connexion with this conclusion it is of interest to consider a conclusion based on entirely different premises for an area having a very different flora and fauna, seasonal variation and conditions for growth.

In surveying the plankton of Kiel Bay in order to determine the relation between animals and plants, Lohmann (1908) employed methods whereby samples of the total plankton down to the minutest organisms were obtained. He computed the total volume of the plankton organisms by displacement with scale models of each species. As a result he was able to give a complete picture of the plankton community throughout the year and concluded that in December, January and February the plants made up less than one-third of the total volume, in November and March their proportion was between one-third and one-half, and in the remainder of the year the plants formed one-half to three-quarters of the volume of the plankton. On the basis that all Metazoa required a daily ration of one-tenth of their own volume and supposing that always only one-third of the mass of producers present was destroyed then there would be a deficit in January and February, but for the remainder of the year there would be a surplus.

It is also of interest to compare the summer population of plants in the L4 area with that in Loch Striven. The growth of diatoms in Loch Striven during the summer of 1926 (Marshall and Orr, 1927) was in several ways different from the growth at L4 in the summer of 1933 and 1934.

The population of diatoms only once reached a really low level (on July 14th) for a short period and for relatively long periods they were abundant. Both in the Loch, and at L4 in 1934 there appears to have been a sufficiency of nutrient salts, brought into the upper layers from below, throughout the summer. At the end of May and beginning of September very little phosphate in the surface layers in Loch Striven is shown by analyses, but this is not reflected in the number of diatoms. The upper 45 metres of water was richer in phosphate than that at L4 and the water below 45 metres very rich, averaging some 24 mg. P per cubic metre during the summer.

The spring outburst of Skeletonema had disappeared by April 20th 1926, on which date polychæte larvæ were abundant. This may be significant since the end of the spring outburst at L4 in 1933 was likewise marked by an abundance of these larvæ. By April 27th they had disappeared and a recrudescence of Skeletonema commenced, reaching its maximum on May 18th when its numbers rapidly fell and its place was taken by several species of Chætoceros and Thalassiosira, which had for the most part developed while the Skeletonema were becoming less numerous. In their turn these "disappeared" by June 10th. Their further development was doubtless impeded to some extent by lack of phosphate.

This first secondary outburst was followed by a second short-lived outburst commencing at the end of June and lasting only some ten days. It was composed of Chætoceros, Cerataulina and Skeletonema.

On July 14 the diatom population was at a minimum and on this day lamellibranch larvæ were found in great abundance in the tow-nets.

Towards the end of July a third outburst of diatoms commenced and lasted until the middle of September. During this period of abundant diatoms, it should be mentioned that, at intervals copepods and, on August 20th, lamellibranch larvæ were found in abundance.

At L4 during the latter part of July and August in 1934 the numerous animals kept the diatoms grazed down to a low level ; in Loch Striven, in 1926, the animals did not. In the summer of 1930 Moore found only a few diatoms deposited on the bottom of this loch compared with the quantity deposited immediately after the spring outburst. If the latter were only a minority of the spring outburst, then only a minority of the summer production escapes being eaten. A considerable deposit of fæcal pellets composed of diatom remains took place throughout the summer.

AUTUMN AND WINTER CONDITIONS.

In the middle of September a rapid increase in the population of diatoms took place. A maximum was found before the end of the month and the outburst "disappeared" before the end of October. It is seen from

Figure 8 that the autumn and winter of 1934 and 1933 were very dissimilar. The latter part of October and all November, 1934, were dark and overcast, unlike the previous year when November was sunny and bright.

It appears that the extent and duration of the autumn outburst depends largely upon weather conditions—illumination—as had been noticed by Herdman.

This autumn outburst consisted mostly of several species of Chætoceros, whereas in 1933 Rhizosolenia and Biddulphia were dominant.

In both years the phosphate in the water had started to increase some weeks previous to the autumn outburst of diatoms, and in 1934 a considerable supply had been available since August 24th, available for some three weeks prior to any material increase in diatoms. We have no estimates of the nitrogen salts in the water, but previous investigations have shown that nitrite and nitrate are regenerated a little later than phosphate. It has been found for one species of diatom that its *rate* of growth is greatly increased by increasing the concentration of nutrient salts when these are present in small quantity, although there may have been sufficient for a considerable growth at the lower concentrations.

Although an increase in phosphate took place some time before, it is probable that an increase in nitrogen salts did not occur before early September.

The survey has in general indicated that a change in diatom population is brought about by a change in one or both of two opposing factors—the rate of growth of the diatoms (depending upon illumination and probably concentration of nutrient salts) and the rate at which the diatoms are eaten (depending upon the number and kind of herbivorous animals).

During the September period when the population of diatoms was rapidly increasing, the animal population was very high. On the 21st, when the maximum population of diatoms was found, the animals were almost at a maximum. That they were not feeding freely upon the numerous diatoms is suggested by the number of fæcal pellets per animal being similar to the numbers in July and August when diatoms were very sparse, and by examination of the animals showing very few to contain food in contrast to the large numbers of cirripede nauplii and Temora found feeding earlier in the year.

The early autumn community of numerous animals allowed a considerable population of diatoms to be built up during the third week in September and did not start to feed freely upon them until later in the month. Then and during October the numbers of animals were much less.

Our thanks are due to Mr. G. M. Spooner for making various statistical analyses in connexion with the diatom counts, to Miss S. M. Marshall for supplying original data of the Loch Striven survey, to Dr. H. B. Moore for data concerning the deposition of fæcal pellets in Loch Striven, to Professor A. C. Hardy and to Mr. Lucas for data concerning the distribution of plankton in the North Sea and the experimental feeding of plankton animals, to Miss P. M. Jenkin for data concerning the growth of diatoms at different depths over a 24-hour period and to Dr. W. R. G. Atkins for data concerning illumination.

SUMMARY.

Vertical hauls between surface and 45 metres depth were made with a measuring net, throughout 1934, at a position 5 miles S.W. of Plymouth Breakwater in *circa* 50 metres depth of water.

The phytoplankton organisms were counted and also assessed from their content of plant pigments.

A close relation was found between numbers of diatoms and their pigment contents after making allowance for the small size of three species.

The phosphorus content of the phytoplankton was estimated on several occasions.

The zooplankton organisms per cubic metre of sea were counted and estimations were made of their phosphorus content.

The diatom population differed from that found in 1933, in which year the spring outburst was shorter but more intense, the sporadic summer outbursts were more intense, the autumn one lasted longer; and more phosphate was utilised by the plants during the first half of the year.

Evidence is presented that the spring outburst of diatoms is limited in quantity and time by the grazing of the herbivorous plankton animals.

Some species of these herbivores appear to eat greatly in excess of their needs when diatoms are abundant.

No evidence was found that the herbivores are reduced in numbers by lack of food during late summer, and a calculation suggests that there was always a sufficient daily production of vegetable matter for their metabolic needs.

The duration of the autumn outburst of diatoms appeared to be controlled by the amount of light available.

Calculations gave a maximum value for the average rate of growth of diatoms in the sea in spring. This value lies between observed rates.

Only a fraction of the phosphate utilised by phytoplankton during the first half of the year has been found as phosphorus compounds in the planktonic population. It is considered that much of the organic phosphorus compounds in diatoms may pass undigested through animals and remain in solution in the sea until regeneration to phosphate takes place in late summer.

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Seasonal Changes in the Ovary of the Immature Hake, *Merlucius merluccius L.*

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With 5 Figures in the Text.

THE major seasonal changes in the weight and " condition " of the somatic tissues of mature fish are attributable to spawning ; they take the form of a seasonal cycle, in which, starting from a point of optimum condition, there is a progressive loss of condition due to the transference of material from the somatic tissues to the ripening gonads, followed by a recovery to the optimum condition after the spawning act is completed and while the gonads remain quiescent, or slowly begin to recover.

In at least four species of fish, namely, Cod, Haddock, Hake and Pilchard, the seasonal changes of condition in the somatic tissues found in the adult fish are foreshadowed in the immature fish, in which the gonad does not yet annually produce a large crop of eggs or spermatozoa, and in which therefore there is no apparent call by the gonad on the reserves of the fish. Graham (1923) using data published by Russell (1922) demonstrates this phenomenon in the Cod, and Russell's data on the Haddock (1914) show the fish of 25 cm., which consist mainly of immatures, show a loss of condition at the season when adult fish are losing condition during the ripening of the gonads. Ramalho (1932) shows that Pilchards of 13 cm. show the same seasonal changes in condition as the adults, and I have shown (1930) that the seasonal changes in the condition of the somatic tissues of immature and adolescent female hake, which do not spawn, foreshadow closely the metabolic rhythm of adult hake.

Now the gonad also of the adolescent female hake shows seasonal changes very closely foreshadowing those of the mature female, and in the present paper a seasonal rhythm of activity, resembling that which occurs in the gonad of mature and adolescent hake, will be suggested for undoubtedly immature female hake.

It has not been possible to work with immature male hake also, for the male matures as early as the 20 24-cm. length group, and hake of this length are rarely and irregularly taken in the nets of commercial steam-trawlers. The female hake, on the other hand, does not become adolescent until at least 50 cm. in length, and is not mature until 70 cm. (Hickling, 1930 ; Birtwistle and Lewis, 1925) so that the collection of material for an investigation of the gonads of immature female hake has been an easy matter.

A. The Material.

The material and observations have been collected at sea, mainly during my voyages on hake research aboard steam-trawlers fishing for hake to the south and west of Ireland, but also during the annual surveys carried out in August, 1930, and August, 1931, in the Ministry of Agriculture and Fisheries' research vessel, *George Bligh*. There is available a series of samples of undoubtedly immature hake ovaries collected as follows :—

	Vessel.	Date.	Region.
1.	*Lowther*, Fleetwood	March, 1930	West of Scotland.
2.	*Sasebo*, Cardiff	May, 1930	West of Ireland.
3.	*George Bligh*	August, 1930	South of Ireland.
4.	*Tenedos*, Milford	October, 1930	South of Ireland.
5.	*Trawler Prince*, Milford	December, 1930	South of Ireland.
6.	*Tenedos*, Milford	January, 1931	South and west of Ireland.
7.	,, ,,	April, 1931	South and west of Ireland.
8.	*Redgauntlet*, Fleetwood	June, 1931	West of Ireland.
9.	*George Bligh*	August, 1931	South of Ireland (Labadie Bank).
10.	,,	,,	West of Ireland (Galway Bay).
11.	,,	,,	North-west of Ireland (Black Rock).
12.	*Lily Macrae*, Milford	November, 1931	South of Ireland.
13.	*E and F*, Milford	February, 1932	South and west of Ireland.

Each of these thirteen samples consists of fifteen ovaries, namely, five ovaries of hake of 35–39 cm., five of hake of 45–49 cm., and five of hake of 55–59 cm. The ovaries were fixed in Bouin's fluid, and later were cut into sections and stained with iron hæmotoxylin and eosin at the Lowestoft Laboratory by Mr. B. G. Clarke, Chief Laboratory Assistant, to whom here I would express my thanks.

In addition to these samples of ovaries, during the cruises when samples 3, 6, 7, 8, 9, 10, 11 and 12 were collected, a large number of determinations of the volume of immature hake ovaries were carried out. The determination was made simply by observing the displacement of water in a measuring cylinder. The results are given in Table IV at the end of this paper.

B. CYTOLOGICAL CHANGES IN THE OVARIES OF IMMATURE HAKE.

The nuclear changes accompanying the development of the egg in the hake will now be briefly described, with the help of Wilson's authoritative text-book (1925).

Oogonial divisions have not been seen in any of the sections examined, and all oogonial divisions have been completed by the time the hake has attained a length of 35–39 cm., when about four years old. A few ovaries of hake of 25–29 cm., which are approximately three years old (Hickling, 1933), were also examined, and in them also there was no sign of oogonial divisions. But such ovaries were full of " nests " of oocytes, showing that oogonial division had only recently been completed. It can safely be said that oogonial division is completed, in the hake, by the fourth year of life (when three years old), and the young ovary then contains only vast numbers of oocytes.

[In order to avoid confusion in this paper, the term *oogonia* is taken to refer, as Wilson himself implies in his Figure 135, to germ-cells still capable of division to form new germ-cells like themselves; the end products of oogonial divisions no longer divide, but are the starting point of oocyte growth or maturation, and are better themselves referred to as oocytes. This term should, in my opinion, also include those cells, sister-cells of the oocytes, which form the accessory or follicle-cells in older ovaries, and which, in Wheeler's view (1924) are capable of metamorphosis back into oocytes and are thus potential oocytes.]

The oocytes observed in my sections are in the " resting " or net-like stage (Figure 1, A A). They are minute, and present in vast numbers just beneath the surface of the ovigerous lamellæ. No cytoplasm can be seen, the chromosomes are thin and stain only palely with iron hæmatoxylin, and there are several strongly basophilic nucleoli, of which one may be more conspicuous than the others.

In the first stage of maturation, there is a single deeply-staining nucleolus, and the chromosomes appear more strongly basophilic and somewhat thicker and so more conspicuous (Figure 1, B B). The cytoplasm becomes visible as a very thin envelope around the nucleus. I shall refer to this stage of development as that of the " pre-synaptic egg " : they are easily visible in sections on account of their conspicuous nucleolus. The change to the pre-synaptic egg is accompanied by a considerable increase in size; it should be mentioned that, in Figure 1, the drawings of oocytes (A A) are on a larger scale than those of the pre-synaptic and later stages.

This pre-synaptic stage leads on to synapsis (Figure 1, C). The large nucleolus lies to one side of the nucleus (which cannot be clearly differentiated from the cytoplasm) and the chromosomes appear as a bunch of thick, very deeply staining threads. My sections were not designed to give minute cytological detail, so I cannot say how many chromosomes appear, and whether or at what stage they become ranged in pairs. The chromosomes, however, appear to be definitely polarized. Nuclei in synapsis are easily recognisable in sections, even under relatively low magnification.

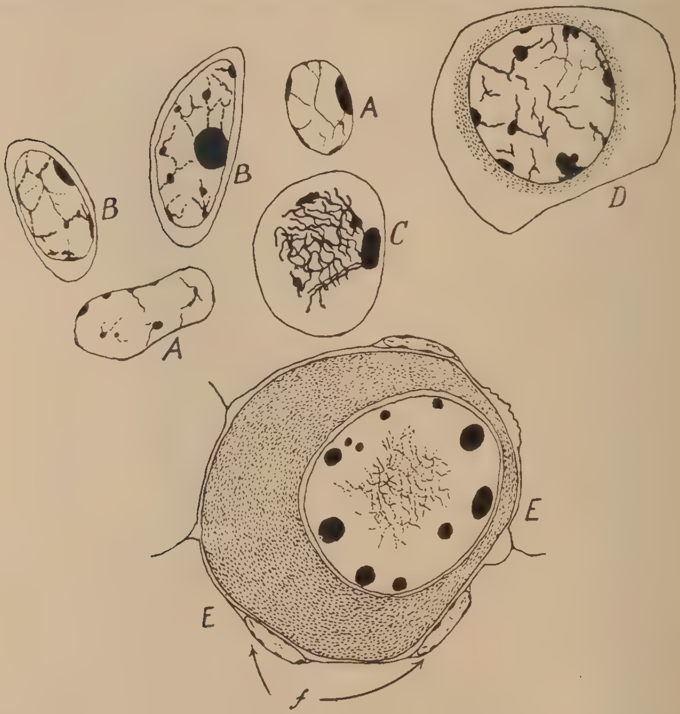

Fig. 1.—Successive stages in the change from the resting oocyte (A A) to the young egg (E). A A on larger scale than rest of drawings: explanation in text, Section B (f. Follicle nuclei).

The next stage (Figure 1, D) is accompanied by an enlargement of the nucleus; the chromosomes stain less deeply and separate, and a number of deeply staining nucleoli appear. The cytoplasm increases greatly in relative volume, and a ring of deeply staining matter appears in the cytoplasm about the nucleus. Here again my material does not allow me to say anything definite about the origins of the cytoplasmic changes in the egg.

Finally (Figure 1, E) the nucleus becomes still more enlarged, the chromosomes lie loosely in the centre of the nucleus, staining so palely as to be barely visible, while the nucleoli increase in size and number and arrange themselves at the periphery of the nucleus. From this point onward the nucleus remains quiescent, while it is the turn of the cytoplasm to show a series of changes. Eggs in which the nucleus has reached the stage shown in Figure 1, E, are termed " post-synaptic eggs," or " young eggs."

Eggs in the stage shown in Figure 1, D, have been regarded, some as synaptic, others as post-synaptic eggs. It will be obvious that no hard and fast line can be drawn between stages which in reality pass smoothly from one to the other; the classifications adopted in this paper are necessarily arbitrary.

It has already been said that, from the stage shown in Figure 1, E, the nucleus remains quiescent while the cytoplasm shows a series of changes. First the cytoplasm becomes densely basophilic throughout, except for a thin clear zone immediately outside the nuclear membrane. It also rapidly increases in volume, and the follicle now becomes apparent. In Figure 1, E, three follicle nuclei may be seen in contact with the developing egg (F). Next, the volume of the egg steadily increasing, a ring of oil globules appears in the cytoplasm near the nucleus. During the preparation and staining of sections this is dissolved away and is then manifested only as a reticulation of the cytoplasm. Finally, yolk granules appear, the follicular epithelium becomes fully developed, and the whole egg becomes opaque. The formation of yolk granules in a considerable number of the eggs in an ovary, or even of oil droplets in a large proportion of them, changes the naked-eye appearance of the ovary from a clear pale yellow to a turbid yellow, or a turbid yellowish red flecked with pink dots ; an ovary having this appearance is no longer classed as immature and so passes out of the scope of this paper. Ovaries in these later stages have been fully dealt with elsewhere (1930). We are now concerned only with ovaries containing oocytes, and eggs in the pre-synaptic, synaptic and early post-synaptic stages ; ovaries which are, by their naked-eye appearance, classed as immature.

C. Seasonal Changes in the Occurrence of Synapsis.

Synapsis is clearly an important phase in the development of the egg, namely, the passing over from the quiescent oocyte stage to the young egg stage. It marks the addition of new young eggs to the general egg-stock in the ovary.

Now the cytoplasmic changes occurring in the eggs contained in the ovary of a mature hake are definitely seasonal (Hickling, 1930) and are manifested in the conspicuous changes described as the spawning-cycle.

But the nuclear changes undergone in synapsis are a necessary preliminary to the cytoplasmic changes which are later initiated. It will be our present object to find whether these nuclear changes also show a seasonal cycle of activity.

It has already been said, in Section A, that a series of samples of immature hake ovaries were collected at different seasons of the year, each sample consisting of fifteen ovaries, namely, five each of hake of 35–39, 45–49 and 55–59 cm. respectively. Sections of these ovaries were examined for nuclear activity in two distinct ways.

The first method was to make a traverse of each section, along its greatest diameter, under $\frac{1}{6}''$ objective, by means of a mechanical stage, and to count the number of nuclei in synapsis encountered in the field of view during the traverse. This might be expected to give a good estimate as to the extent to which synapsis is occurring in each ovary, provided that the nuclei in synapsis are fairly evenly distributed throughout the ovary, and also that all ovaries from fish of the same length-groups have roughly the same diameter. But the diameter of sections of ovaries of fish of the same length-group in the same sample varies considerably. Moreover, as the ovary enlarges with the growth of the fish, the ovigerous lamellæ become bigger, and therefore the young eggs, which lie immediately beneath the surface of these lamellæ, become irregularly scattered. A traverse of a section of the ovary from a fish of one of the larger length-groups is therefore not satisfactory as a method of assessing the relative amount of synapsis occurring. However, the rough estimate of the absolute numbers of nuclei in synapsis obtained by this method is a check on the results of the second method.

The second method was to classify an unselected sample of about 400 nuclei in each section into the three classes, "pre-synaptic," "synaptic" and "post-synaptic," or about 60,000 nuclei in all. No attempt was made to count the immense numbers of minute resting oocytes, and the nuclei were classified according to the definitions given in Section B. This method gives the percentage frequency of each class of nucleus in the unselected sample. It has the advantage over the first method of being independent of the diameter of the ovary, and of giving a more standardised estimate, but the disadvantage of giving relative frequencies only. Thus, if the percentage frequency of nuclei in synapsis is found to decrease in the summer months, as compared with the winter months, it does not necessarily follow that the process of synapsis is then less active. A simultaneous progressive increase in the percentage frequency of the other two classes of nucleus might equally well account for such a decrease.

Personal bias was guarded against in all cases by the replacement of the label bearing the date of collection by one bearing a serial number.

The results of the first method are given in Table I. The samples were examined in two batches, the first including those collected from March, 1930, to January, 1931. Further samples were then collected, from April, 1931, to February, 1932. It will be noticed, in Table I, that the average number of nuclei in synapsis per sample is much greater in the second than in the first batch, especially among the large fish of 45 49 and 55–59 cm. This is probably because, with greater experience, the nuclei were classified with greater confidence. In spite of this discrepancy, however, I have included the original figures in Table I.

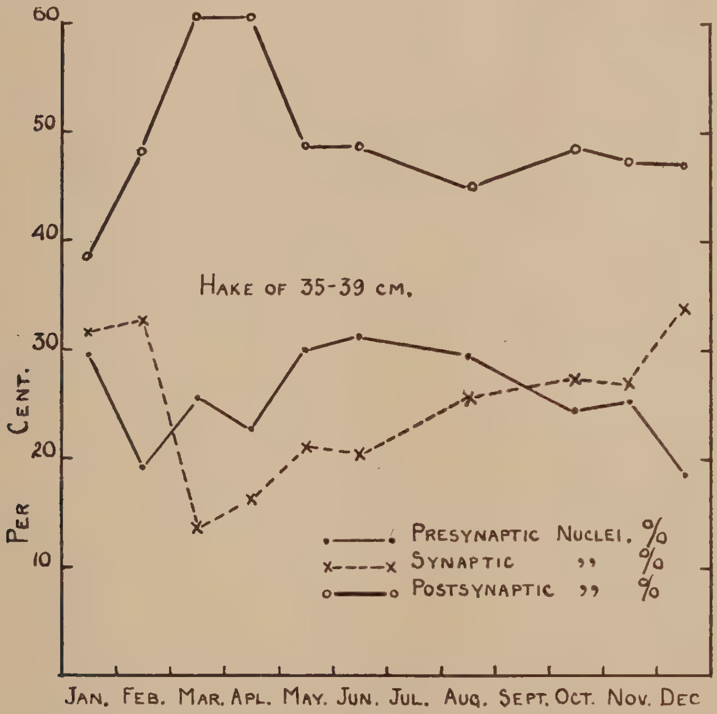

FIG. 2.—Seasonal change in the percentage frequency of nuclei in the three stages, in immature hake of 35–39 cm. Data in Table I.

The results of the second method of examination are given in Table II. The samples were examined all together when the collection was complete. The results are much more consistent than those derived from the first method, and will be considered first. These are shown graphically in Figures 2 and 3. The consistency between all samples is such that the results from 1930, 1931 and 1932 can be grouped together as though they had all been collected in successive months in one calendar year, and they

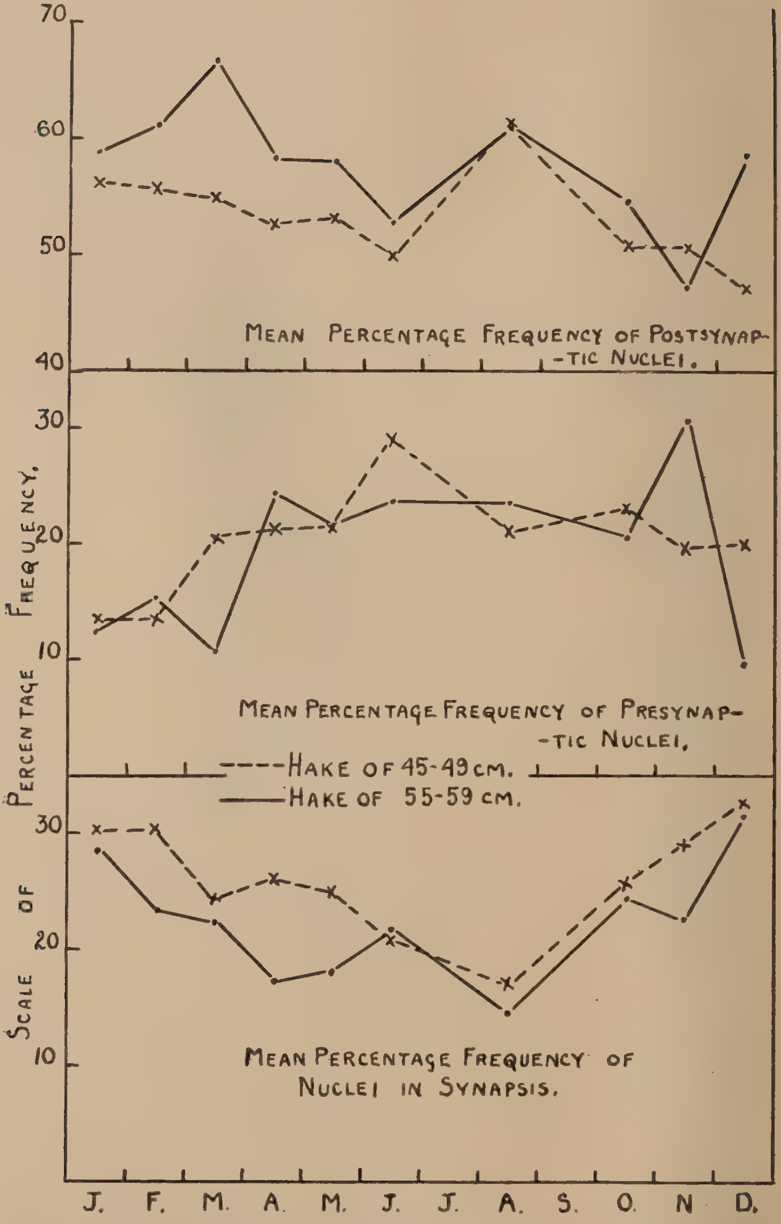

Fig. 3.—Seasonal change in the percentage frequency of nuclei in the three stages, in immature hake of 45–49 and 55–59 cm. Data in Table I.

are so represented in Figures 2 and 3. The mean of the four August samples is taken as the figure for August.

In Figure 2 are plotted the points representing the mean percentage frequency of pre-synaptic, synaptic and post-synaptic nuclei in ovaries of hake of 35–39 cm. in the samples.

The plotted points are joined by straight lines.

Nuclei in synapsis show a minimum percentage frequency in March, followed by a regular rise to a maximum in December. In January and February the percentage frequency remains high, and then there is a sharp drop to the minimum in March. Pre-synaptic nuclei have their minimum percentage frequency in February, and show an increase until June, when they decline again to a low value in December The percentage frequency of pre-synaptic nuclei drops from June until December as the percentage of synaptic nuclei rises, as indeed might be expected, since the pre-synaptic stage leads directly on to synapsis. The high value for pre-synaptic nuclei in the January sample is, however, anomalous in this respect.

Post-synaptic nuclei increase in percentage frequency from January to March and April, decline in May and remain steady for the rest of the year. Since the high values for post-synaptic nuclei follow immediately after the highest values for synaptic nuclei, it is probable that these high values also actually mark the addition of new post-synaptic eggs to the general stock of such in the young ovary. The later decline in the percentage frequency of post-synaptic nuclei, however, is probably due to the increase in the combined frequencies of pre-synaptic and synaptic nuclei.

In Figure 3 the seasonal changes in the precentage frequency of nuclei in each stage in the ovaries of hake of 45–49 and 55–59 cm. are shown ; in order to avoid crowding the diagram the graphs for each class of nucleus are drawn separately.

The seasonal changes in the percentage frequency of nuclei in the synaptic stage agree sufficiently well for both length-groups to be represented in the same diagram. The correlation coefficient between the changes in hake of 45–49 and 55–59 cm. is 0·68, an agreement which would be obtained by chance in uncorrelated data only once in a hundred trials with the number of observations available (Fisher, 1930).

Nuclei in synapsis, in hake of 45–49 and 55–59 cm., form the greatest percentage of the nuclei in December, January and February (as in hake of 35–39 cm.). The percentage frequency then declines to a minimum value in August (instead of in March, as in hake of 35–39 cm.) after which it rises again to the high winter values. Pre-synaptic nuclei have low values in January and February, but from March to June the percentage frequency rises. From June to September (disregarding the high value in hake of 55–59 cm. in November) the percentage frequency of pre-synaptic nuclei declines somewhat. This agrees with the behaviour of pre-synaptic nuclei in hake of 35-39 cm. Post-synaptic nuclei have high values from December to March (in fish of 55-59 cm.) and from January to, say, March (in fish of 45–49 cm.) and then decline throughout the year except for a high value in both cases in August.

In all classes of immature female hake, nuclei in synapsis, while present in the ovary throughout the year, have a definite seasonal cycle of relative abundance, being relatively most abundant in the winter months of December, January and February. Hake of 35-39 cm. differ from hake of 45–49 and 55–59 cm. in showing a minimum relative abundance in March, immediately following the time of maximum relative abundance, whereas the latter show a time of minimum relative abundance in August. These findings should now be compared with the results of the first method of examining the material, namely by the counts of the actual numbers of nuclei in synapsis observed during a traverse along the longest diameter of each ovary-section. The average numbers of nuclei in synapsis in the ovaries of hake of each length-group in each sample are given in Table I.

In hake of 35–39 cm. the numbers of nuclei in synapsis increase from 13 per ovary-section in March, 1930, to a maximum of 83 per ovary-section in January 1931. There is then a sharp drop to 28 per ovary-section in April, 1931, followed again by an increase to a fresh maximum in November, 1931, and February, 1932. (The average of the three samples collected in August, 1931, is here considered.) Clearly, as far as hake of 35–39 cm. are concerned, both the relative and the absolute numbers of nuclei in synapsis are greatest in the winter months, and fall to the minimum in March and April.

In hake of 45–49 and of 55–59 cm. the changes in the average numbers of nuclei per ovary-section from sample to sample are very similar to one another. In the first batch of readings the average number of nuclei in synapsis rises from March to May, 1930, then falls to August and October, 1930, rises again sharply to December, 1930, and falls in January, 1931. In the second batch of readings a more definite trend is shown by the samples. The average number of nuclei in synapsis falls from April, 1931, to August, 1931, and rises again to high values in November, 1931, and February, 1932. The second series of readings, in ovaries of hake of 45–49 and 55–59 cm., shows the same seasonal trend in the absolute numbers of nuclei in synapsis as in their relative numbers (Table II), though the first series does not.

In my view, therefore, there is reason for believing that the important process of synapsis, which marks the change from the quiescent oocyte to the young egg, is most active in the winter months. The data in

Table II and in Figures 2 and 3 also suggest that the process is initiated in the period January to June by the appearance of pre-synaptic nuclei, presumably by metamorphosis of a certain proportion of the resting oocytes. The pre-synaptic nuclei pass over into synapsis, which reaches its maximum activity in the months from December to January. Synapsis leads to the formation of post-synaptic eggs, or young eggs, which accordingly show their greatest relative abundance from January to April.

D. Seasonal Changes in the Mean Diameter of the Eggs.

In Section C evidence was shown that, as the result of a seasonal cycle in the intensity of the process of synapsis, there is a seasonal change in the rate of addition of new young eggs to the general egg-stock contained in the ovary, the addition of new young eggs being most active in the months from January to April. This addition of new young eggs might be expected to lower the average diameter of the stock of post-synaptic eggs in the ovary, thus bringing about a seasonal variation in the average diameter. Accordingly, a large number of unselected eggs were measured along their longest diameter, in the same sections of ovaries as were used, in Section C, for an estimation of the occurrence of synapsis. For each

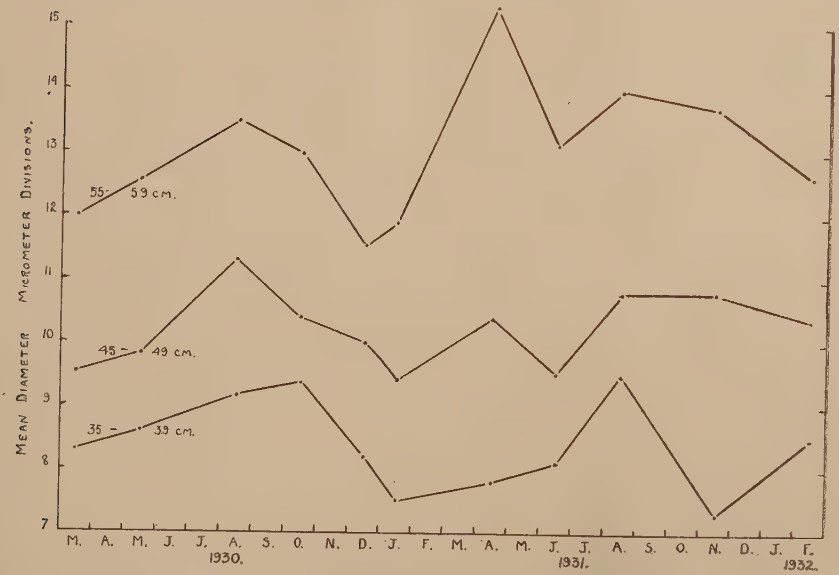

Fig. 4.—Seasonal changes in the mean diameter of the ovarian eggs in immature hake of 35–39, 45–49, and 55–59 cm. Data in Table II.

length-group within each sample the mean diameter of the eggs was calculated, and these are given in Table III. They are shown graphically in Figure 4. Since the samples collected in 1931 give results differing from those collected in 1930, in Figure 4 the results are given in the order of collection of the samples.

In all three length-groups, the mean egg-diameter is low in March, 1930, and then rises to a maximum in early autumn. From this maximum the mean diameter decreases to a minimum in midwinter. From this winter minimum the mean diameter rises to a maximum in April, 1932 (55–59 cm.), or August, 1932 (35–39 and 45–49 cm.), and then declines again. The cycle of changes in 1931 are irregular as compared with 1930 especially in hake of 45–49 cm., but they can still be recognised. It appears that there is a seasonal fluctuation in the mean diameter of the eggs in the ovaries of immature hake, such that the mean diameter is higher in the summer months than in the winter months. Taking the months from October to March as representing the winter months, and from April to August as representing the summer months, there is an increase in mean volume of the egg (calculated from the mean diameter) in the summer over the winter months of 28 per cent in hake of 35–39 cm., of 12 per cent in hake of 45–49 cm., and of 38 per cent in hake of 55–59 cm.

There is a close correspondence between the seasonal changes in the mean diameter of the eggs in the immature and the mature ovary. In Figure 4 it has been shown that the mean diameter of the eggs in the immature ovary tends to be greater in the months from April to August than in the months from September to March. The mature ovary has a low mean weight in the months from October to March, a high mean weight in the months from April to July; the maximum mean weight is found in July (Hickling, 1930). But the changes in mean weight of the mature ovary are due to the growth of the current season's crop of ripening eggs, which undergo an immense increase in diameter and volume. In the immature ovary this growth in the diameter of the eggs carries them, in the larger immature ovaries, to the point of incipient formation of oil in the cytoplasm. Further than this they cannot go, for where a large number of the eggs enlarge and secrete oil, and still more, yolk, the naked-eye appearance of the ovary changes, and it becomes by definition adolescent or mature.

A correlation can be shown between the mean volume of the eggs contained in the immature ovary (calculated from the mean diameter D by the approximation, Volume$=\frac{D^3}{2}$) and the mean volume of the ovary.

In Table IV are given the mean volumes of the ovaries of immature hake of 35–39 and 45–49 cm., as determined by displacement, during certain of the voyages in which samples of ovaries were obtained. Insufficient numbers of immature hake of 55–59 cm. were available to obtain reliable mean volumes of the ovaries of this length-group also.

In hake of 35–39 cm., the correlation coefficient between the mean volume of the egg and the mean volume of the ovary is 0·81 ; a correlation as good as this would be obtained by chance in uncorrelated material between once and twice in a hundred trials (Fisher, 1930). In hake of 45–49 cm. the correlation coefficient is 0·76 ; a correlation as good as this would be obtained about twice in a hundred trials by chance in uncorrelated material. Changes in the mean volume of the eggs therefore cause changes in the mean volume of the ovary, which therefore, in immature hake, tends to be slightly larger, relatively to the fish, in summer than in winter.

E. DISCUSSION.

Seasonal changes can be demonstrated in the ovaries of undoubtedly immature female hake. The nuclear changes undergone in synapsis, during which the quiescent oocyte metamorphoses into the young egg, while occurring throughout the year, reach a maximum in the winter months (December, January, and February). The addition thereby of a new batch of young eggs to the stock of eggs already accumulated in the ovary lowers the mean diameter of the eggs in this stock ; with the slackening off of synapsis during the summer the mean diameter of the eggs in the immature ovary increases as the new eggs grow up into the general egg-stock. The increase in mean diameter of the eggs causes an increase in the mean volume of the whole ovary, which is greater, relatively to the length of the fish, in summer than in winter.

These seasonal changes in the ovaries of immature hake foreshadow those which have been found to occur in the ovaries of mature hake. In mature fish also there is an addition, in the winter months, of a new batch of young eggs to the reserve stock in the ovary (Hickling, 1930), and in them also there is in summer an increase in the mean diameter of the eggs as a quota of the reserve fund of eggs undergoes an immense increase in diameter and volume during maturation. In mature fish these eggs are ripening for spawning in the early summer months. [In my previous paper I could detect no seasonal variation in the mean weight of the ovaries of immature hake, but such seasonal variations as I have shown in the present paper would affect the mean weight of the immature ovary only to a trifling degree, well within the experimental error of weighing carried out at sea with a spring-balance.]

Such a foreshadowing, in the immature ovary, of the seasonal changes occurring in the mature ovary has been recorded in a freshwater Cottus (*Cottus bairdii* Girard) by Hann (1927). This is a small fish with a short life-history, the female maturing at the end of its second year of life. But the ovarian cycle can be detected in the first year of life, while the fish is definitely immature.

The conclusions reached in this paper, in conjunction with those reached in my previous papers on the seasonal changes in the ovaries of adolescent and mature hake, and on the growth-rate (1933), may be used to present an account of the later ovarian development of this fish.

By the end of the third year of life at latest, when the fish is 25–29 cm. in length, the division of the oogonia has been completed, and the ovary is full of resting oocytes, of which, even at this stage, many have metamorphosed into young eggs. In each subsequent winter, a fresh batch of resting oocytes becomes active, undergoes synapsis, and in the following summer grows into the " stock " of eggs in the ovary. In each subsequent summer also a few of the eggs may show incipient development, leading to an increase in size and to the appearance of oil globules in the cytoplasm. By the seventh year of life, when the fish is about 55–59 cm. in length, this incipient cytoplasmic development takes place on a considerable scale, and at 65–69 cm. (Table V and Figure 4, in my 1930 paper) when in its eighth year of life, this enlargement of a portion of the reserve fund eggs, with the secretion of oil, and even of yolk, changes the naked-eye appearance of the ovary, which is now classed as adolescent. Adolescent ovaries show a seasonal fluctuation in weight such that this is high from April to August, and low from October to March. But adolescent ovaries do not produce ripe eggs, and the advanced eggs are re-absorbed at the close of the season of adolescence. Finally, at about 75–79 cm., when in its ninth or tenth year of life, the enlargement of a portion of the eggs, and the secretion in them of oil and yolk, leads to the complete development of the eggs and so to spawning, which occurs mainly in the months from April to July.

If the results set out in this paper are accepted, clearly the seasonal rhythm of activity in the ovary of the hake, which in the mature fish is manifested as the spawning cycle, is already established at an early stage in the life-history of the fish, many years before maturity is attained. I have already shown (1930) that a seasonal rhythm of activity in the somatic tissues of the hake is present in immature fish. In Figure 5 are shown (continuous lines) the graphs for the quarterly changes in mean volume of the eggs in the ovaries of immature hake of 35–39, 45–49, and 55–59 cm. (the data in Table II having been recalculated as quarterly averages, and the volume calculated from the approximation $\text{Volume} = \frac{\text{Diameter}^3}{2}\Big)$. The broken line shows the quarterly changes in mean weight of the liver of immature female hake of 50–59 cm. (recalculated from the data in Table VIa, 1930). The mean volume of the eggs increases from the first to the third quarters of the year, and then declines in the fourth quarter of the year. The mean weight of the liver decreases from the first to the third quarters of the year and recovers sharply in the fourth quarter of the year. In a mature fish these changes would be interpreted as indicating a transference of material from the liver (somatic tissue) to the gonad. No such suggestion need be made with regard to immature fish ; the graphs simply show that seasonal rythms are present in both somatic tissues and gonad which closely resemble those occurring in mature fish (Figures 1, 11, 17, Hickling, 1930).

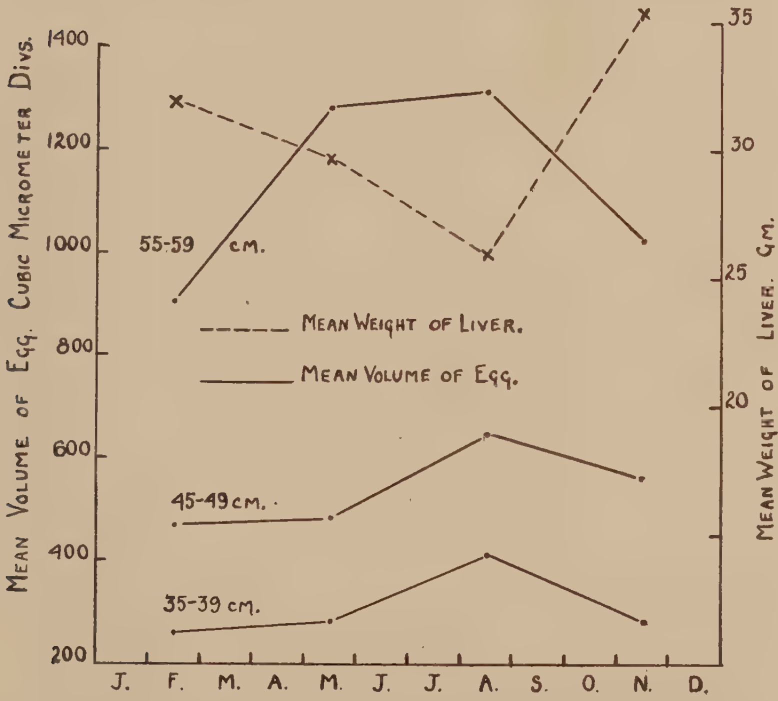

Fig. 5.—Quarterly changes in the mean volume of the ovarian egg in immature hake, calculated from Table II. Also quarterly changes in the mean weight of the liver in immature hake of 50–59 cm., calculated from data in Hickling, 1930.

An interesting point that arises is in connexion with the formation of " growth-rings " in the skeletal structures of fishes, which are so widely used in age-estimation. Graham (1928, ii) found, as a result of a study of the literature, that in no species of fish has a satisfactory relation been shown between the conditions in the external environment and the modification in the growth of the skeletal structures which manifests itself as a growth-ring. He was inclined to think that growth-rate in the cod (which is intimately related with the width of the sclerites in the scale, and so with the manner of growth of the scale) is an "inherent rythmical response," that is, due to an internal factor (Graham, 1928, i). As early as 1907 Dahl had implied an internal rather than an external factor, as connected with the formation of growth-rings in the herring, by his use of the term "physiological winter." But he rejected the possibility that the spawning process could have any connexion with ring-formation because the growth-rings are found to be as well formed in immature as in mature herrings. Schneider (1910) while attacking Dahl's hypothesis, really takes much the same view-point, but suggests that a physiological rhythm may be already present in the immature fish. In my 1933 paper I showed that a growth-ring is formed in the otolith of the hake at the time of greatest exhaustion after spawning, i.e. about October in the mature fish. Immature hake (see Figure 5 in this paper) show the same exhaustion, though they do not spawn. The picture may now be completed by this demonstration, that the physiological rhythm in both gonad and somatic tissues of mature hake are already detectable in immature hake. If the hake is typical of teleosts generally, the fact that immature fish show the same growth-rings as the adult need not in future preclude any hypothesis suggesting that the discontinuous growth of the skeletal structures is associated with the physiological stresses of the spawning cycle.

SUMMARY.

A seasonal variation is found in the ovaries of immature hake (*Merlucius merluccius* L.).

There appears to be a seasonal change in the rate at which young eggs are formed from resting oocytes, as indicated (1) by the change in the relative abundance of nuclei in synapsis, and (2) by the change in the average diameter of the eggs in the egg-stock in the ovary. These processes show considerable correspondence in their season of incidence with the ovarian cycle of the mature and adolescent fish.

A physiological rhythm has now been detected in both somatic tissues and gonad in the immature hake, which foreshadows the physiological rhythm associated with the spawning cycle in the mature hake. The implication of this on the question of the formation of "growth-rings" in the skeletal structures is briefly discussed.

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TABLE I.

AVERAGE NUMBER OF NUCLEI IN SYNAPSIS ENCOUNTERED DURING TWO TRAVERSE OF THE OVARY-SECTIONS.

Samples.	March, 1930. Lowther.	May, 1930. Sasebo.	Aug., 1930. G. Bligh.	Oct., 1930. Tenedos.	Dec., 1930. Trawler Prince.	Jan., 1931 Tenedos.	April, 1931. Tenedos.	June, 1931. Red-gauntlet.	Aug., 1931. G. Bligh (Labadie Bk.).	Aug., 1931. G. Bligh (Galway B.).	Aug., 1931. G. Bligh (Black Rock).	Nov., 1931. Lily Macrae	Feb., 1932. E. and F.
Hake of 35–39 cm. . . .	13	28	41	44	53	83	28	67	115	53	51	96	88
Hake of 45–49 cm. . . .	26	36	17	10	47	22	82	65	36	32	16	65	64
Hake of 55–59 cm. . . .	10	29	26	16	28	20	55	53	32	40	40	100	80

TABLE II.

MEAN PERCENTAGE FREQUENCY OF THE THREE NUCLEAR STAGES DEFINED IN SECTION B.

		March, 1930.	May, 1930.	Aug., 1930.	Oct., 1930.	Dec., 1930.	Jan., 1931	April, 1931.	June, 1931.	Aug., 1931. (Labadie Bk.)	Aug., 1931. (Galway B.)	Aug., 1931. (Black Rock)	Nov., 1931.	Feb., 1932.
Hake of 35–39 cm.														
Mean Percentage Frequency of Nuclei in Stages	Pre-synaptic	25·7	30·0	29·9	24·2	18·9	29·6	22·7	31·4	29·1	25·8	34·3	25·4	19·2
	Synaptic	13·8	21·2	24·1	27·2	34·2	31·7	16·7	20·4	27·7	25·5	27·1	27·2	32·7
	Post-synaptic	60·5	48·8	46·0	48·6	47·0	38·7	60·6	48·2	43·2	48·7	38·6	47·3	48·1
Hake of 45–49 cm.														
Mean Percentage Frequency of Nuclei in Stages	Pre-synaptic	20·7	21·6	22·9	23·2	20·0	13·5	21·4	29·1	23·5	16·6	22·0	19·9	13·8
	Synaptic	24·4	25·2	17·5	25·9	32·8	30·2	26·2	21·0	22·9	12·0	16·2	29·3	30·4
	Post-synaptic	54·9	53·2	59·6	50·7	47·1	56·3	52·5	49·8	53·6	71·4	61·7	50·8	55·8
Hake of 55–59 cm.														
Mean Percentage Frequency of Nuclei in Stages	Pre-synaptic	10·7	21·7	23·8	20·6	9·9	12·6	24·4	23·4	23·8	26·2	20·9	30·4	15·4
	Synaptic	22·4	18·3	17·2	24·3	31·6	28·5	17·2	21·9	12·5	18·7	10·3	22·5	23·4
	Post-synaptic	66·9	58·2	58·9	54·6	58·5	58·9	58·4	52·6	63·7	55·1	68·7	47·1	61·2

TABLE III.

Means of the mean Diameters of unselected Samples of Eggs measured in each Ovary (micrometer divisions) (10 div. $= 37\mu$).

Hake of 35–39 cm. . . .	8·3	8·6	9·2	9·4	8·2	7·5	7·8	8·1	9·3	10·1	9·1	7·3	8·5
Hake of 45–49 cm. . . .	9·5	9·8	11·3	10·4	10·0	9·4	10·4	9·5	11·5	9·9	10·9	10·8	10·4
Hake of 55–59 cm. . . .	12·0	12·6	13·5	13·0	11·5	11·9	15·3	13·1	12·6	15·7	13·5	13·7	12·6

TABLE IV.

Mean Volume of Immature Hake Ovaries, determined by Displacement (cubic centimetres).

In hake of 35–39 cm. . . .	1·18	0·71	0·76	0·82	0·80	0·86	1·09	0·86
(No. of Observations) . .	20	20	16	20	22	32	14	15
In hake of 45–49 cm. . . .	3·11	2·53	2·54	3·02	2·03	2·17	2·97	2·11
(No. of Observations) . .	18	17	16	20	20	16	14	15

Erratum in M. V. Lebour's paper on "Balcis":

Page 68, third column, line 36. For "*pernula*" read "*trifasciata*".

Marine Biological Association of the United Kingdom.

Report of the Council for 1934.

The Council and Officers.

Four meetings of the Council have been held in London during the year at which the average attendance has been fifteen. These meetings were held in the Rooms of the Royal Society, and the Council of the Association is indebted to the President and Council of the Society for allowing them the use of the rooms. A Committee of the Council, consisting of ten members, presided over by the Chairman of Council, Prof. E. W. MacBride, F.R.S., visited and inspected the Plymouth Laboratory on April 7th.

A Sub-Committee of the Development Commissioners' Advisory Committee on Fishery Research, consisting of Prof. Graham Kerr (Chairman), Prof. George Barger, Prof. W. W. C. Topley and Sir John Marsden, Bart., with Dr. E. S. Russell as Assessor, inspected the Plymouth Laboratory from July 23rd to 25th and held consultations with four members of the Council of the Association who were present at Plymouth.

The Plymouth Laboratory.

The Laboratory buildings and fittings have been kept in a good state of repair and the paintwork in good condition. The inner walls of a cellar in the new buildings have been coated with waterproof cement, and one of the large windows on the south side of the main laboratory has been renewed during the year. Preparations have been made to replace the ejector used for pumping water into the main reservoirs from the sea by a centrifugal pump driven by an electric motor.

The Aquarium.

The Aquarium has continued to attract a large number of visitors, more especially during the summer months. Several parties of school children have, as usual, studied the animals under the guidance of their teachers. The tanks have been kept well stocked with a representative collection of the local marine fauna, and we have again this year been able to exhibit *Torpedo nobiliana* and *Octopus vulgaris*. Miss M. L. Rothschild kindly presented some living animals, chiefly anemones and corals, from Naples. These made an attractive display in one of the small tanks.

Certain tanks in the Aquarium developed rather serious leaks, but our own engineer and his staff were successful in carrying out the necessary repairs.

The Ship and Motor-Boat.

The steam-drifter "Salpa" and the motor-boat "Gammarus" have worked continuously throughout the year, except for the normal surveys and refits which have been carried out as usual, most of the work having been done by the crew. Both vessels are in good order.

The Staff.

Mr. G. I. Crawford of Trinity College, Cambridge, was appointed Student Probationer and commenced work on April 1st.

Dr. L. E. Bayliss resigned the post of Physiologist at the Laboratory on appointment as Lecturer in the Physiological Laboratory of the University of Edinburgh.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year.

Miss D. Atkins, London (Lamellibranchs).
Dr. J. B. Bateman, Cambridge (Water transfer in Carcinus).
Dr. N. J. Berrill, Montreal, Ray Lankester Investigator, Regeneration of Sabella. Development of Ascidians.
Dr. A. M. Bidder, Cambridge (Cephalopods).
Prof. M. Bogucki, Hel, Poland (Fertilisation of *Nereis diversicolor*).
Dr. J. Yule Bogue, London (Electrotonus and action current in crab's nerves).
L. R. Brightwell, Horsley (Drawings of marine animals).
Dr. L. Bugnard, Toulouse and London (Excitation of fin nerve of Sepia).
K. E. Buxton, London (Diatoms).
Prof. A. Morley Davis, London (Distribution of marine fauna).
J. H. Day, Liverpool (Development of Kefersteinia).
I. Enver, Constantinople and Nancy (General Zoology).
Lt.-Commander W. I. Farquharson, R.N., John Murray Expedition (Oceanography).
Miss R. Fellowes, London (Bacterial diseases in fishes).
Miss M. Finneron, Surrey (General Biology).
Dr. and Mrs. E. Fischer, Frankfurt (Muscles of Balanus, Ascidia, and Crab).
C. M. Fletcher, Cambridge (Mytilus. Physiology of smooth muscle).
Dr. R. W. Gerard, London (Stimulation of the nerve in crabs).
Prof. E. S. Goodrich, Oxford (Polychæta and Porifera).
Dr. H. L. M. Pixell-Goodrich, Oxford (Parasitic Protozoa).
Dr. A. L. Grafflin, Boston, U.S.A. (Blood of marine teleostean fishes).
A. Graham, London (Antedon).

Dr. R. Gurney, Oxford (Copepod parasites of fishes. Decapod larvæ).
Miss B. Harrop, Manchester (Sabella).
C. Hartley, Oxford (Marine food of Spitsbergen birds).
Prof. A. V. Hill, London (Excitation of fin nerve in Sepia, and photo-electric recording of colour changes in Sepia).
Prof. R. Höber, Düsseldorf and London (Crab nerves).
Miss P. M. Jenkin, Cambridge (Correlation of photo-synthesis of diatom cultures in the sea with photo-electric measurements of light penetration).
J. A. Kitching, London (Contractile vacuoles in Protozoa).
Mrs. J. A. Kitching, London (Digestion in Gunda).
Dr. H. Lissner, Hamburg (Herring race investigations).
Dr. O. Lowenstein, Birmingham (Respiration of *Gammarus chevreuxi*).
J. D. Macdonald, Aberdeen, British Association (Decapod larvæ).
Dr. D. C. G. Mackay, Ottawa (Relative growth in *Cancer pagurus*).
Miss D. Mees, Rochester, N.Y. (Regeneration of Sabella).
Dr. H. B. Moore, Port Erin (Biology of Purpura and *Littorina littorea*).
Dr. J. Needham, Cambridge (Metabolism of Mollusca).
Prof. J. H. Orton, Liverpool (Library).
Dr. H. H. Poole, Dublin (Photo-electric measurements of light).
Dr. N. W. Rakestraw, Rhode Island, U.S.A. (Hydrography).
M. Ramadan, Cairo and Cambridge (Crustacean Systematics).
Dr. M. Ramult, Cracow (Development of Sacculina).
Dr. H. Rosenberg, London (Strength duration curve in crab nerve).
Miss M. L. Rothschild, London (Trematodes and trematode larvæ).
D. Scott, New York and London (Crab's nerves).
D. L. Serventy, Cambridge and Western Australia (Gammarus, etc.).
Dr. C. J. Shen, Pekin and London (Post-larval Decapods).
F. G. W. Smith, London (Development of Patella).
J. E. Smith, Manchester (Nervous system of Asteroids).
Miss F. A. Stanbury, Plymouth (Growth of Diatoms).
Miss E. M. Stephenson, Exeter (Colour change in Crustacea).
Dr. and Mrs. K. G. Stern, London (Biological pigments).
F. C. Stott, Heywood, Lancs. (Results of 1933 Oxford University Arctic Expedition).
Prof. C. V. Taylor, California (Protozoa).
Dr. E. F. Thompson, Cambridge, John Murray Expedition (Oceanography).
T. G. Tutin, Kew (Zostera).
A. E. J. Went, London (Herring larvæ).
P. H. F. White, Cambridge (Micromaldane).
Mrs. D. P. Wilson, Plymouth (Marine algæ).
J. Z. Young, Oxford (Physiology of fish and nerves of Cephalopods).
Dr. A. Zoond, Cambridge (Colour change in flatfish).

The usual Easter Vacation Course in Marine Zoology was conducted by Mr. D. P. Wilson and Mr. G. A. Steven, and was attended by forty-four students from Oxford, Cambridge, London, Edinburgh, Sheffield, Newcastle, Manchester, Leeds, Birmingham, and Bristol.

During the Summer Vacation a Course in Marine Biology was conducted by Prof. J. H. Orton, of Liverpool University, with Miss R. Rawlinson and Mr. C. L. Smith as Demonstrators. This was attended by twenty-three students from Oxford, Cambridge, London, Birmingham, and Nancy, France.

Also during the Easter Vacation, Mr. J. M. Branfoot brought six students from Oundle School; Mr. B. A. Barr, four from Harrow; Mr. H. C. W. Wilson, six from Monkton Combe; Mr. A. H. Lewis, four from Wellington College, and Mr. R. N. Aldrich-Blake, two from Bradfield College.

At Whitsuntide, Prof. L. Newton conducted a class of nine students from the University, Aberystwyth, and Mr. W. H. Leigh-Sharpe with Mr. E. Idris Jones, a class of five from the Chelsea Polytechnic.

The Devonshire Association for the Advancement of Science, Literature, and Arts held its 73rd Annual meeting at Plymouth in July this year. On July 4th the Association visited the Plymouth Laboratory and were given demonstrations of the research work by the Scientific Staff.

The Scientific Work of the Plymouth Laboratory Staff.

Physics and Chemistry of the Environment.

The importance of the study of submarine illumination is now becoming more generally recognised and measurements have been made in Swedish waters and on both the east and west coasts of the United States of America. Dr. W. R. G. Atkins and Dr. H. H. Poole of Dublin have continued their collaboration and further time has been devoted to the standardisation of photo-electric cells so that results obtained at different times and in different places may be accurately comparable. Artificial "mean noon sunlight" is suitable for the standardisation of selenium rectifier cells, but for sodium and potassium cells the carbon arc alone gives accurate results on the visual scale. Excellent agreement has been found between the potassium cell carbon arc scale and the "mean noon sunlight" selenium scale when both are used to measure bright mixed daylight. The latter agrees well with the visual scale, whereas the former—in use for the last ten years—was thought to be rather too high. It has now been shown to be in close accord with the visual scale. Moreover, the constancy of the cells has been established over a period of six years.

The measurements made hitherto refer to the illumination received upon a plane surface set at any desired angle with respect to the source. For plant photosynthesis, however, what is most important is the total illumination, regardless of angle. To measure it a globe integrating photometer has been devised; this has internal diffusing surfaces so arranged that its readings are independent of the altitude and azimuth of the source of illumination save for unimportant irregularities occasioned by the lack of uniformity in the diffusing media.

Further measurements have been made at sea in connexion with Miss P. M. Jenkin's work on diatom photosynthesis at various depths. Work has also been carried out at Station E1 using a large number of colour filters in an attempt to analyse more accurately the spectral composition of the light at various depths. This involved so many depth series that it was only rendered possible by the modification of the apparatus described in the last issue of the Journal.

The latest modification in the circuit of the potentiometer-amplifier-telephone null method used at sea has restored to the rectifier cell many of the advantages of the emission cell, without sacrificing its own special advantages, so that its effective sensitivity has been increased, temperature errors much reduced and the curvature of the light/current characteristic rendered far less important.

Dr. L. E. Bayliss also has been investigating the possibility of developing a photographic method for integrating the total quantity of light received on a surface during a long interval of time. The method consists essentially in making a print of a standard neutral-tint wedge and determining the density of the wedge at the point where the print has a standard density, thus measuring the average intensity of the light received in terms of the intensity of some standard source. For convenience at sea and in the field, it was decided to make the prints on P.O.P. and much time has been spent in endeavouring to discover whether this paper obeys the reciprocity law with sufficient exactness. Some difficulty has been experienced in obtaining a sufficiently powerful and uniform source of light, and the accuracy of the method has not yet been definitely ascertained. Some measurements have, however, been made at sea in conjunction with the work of Miss P. M. Jenkin on the photosynthesis by marine diatoms.

Hydrographic data have been collected in the mouth of the English Channel throughout the year, continuing the observations which have been made since 1921. The early part of the year was marked by the extension of high salinity Atlantic water into the mouth of the Channel, and, apparently, rather unusual movement of the water masses in the Plymouth area, where more intense sampling than hitherto was carried out in connexion with a plankton survey. The data will be worked up by Mr. H. W. Harvey when all relevant observations by this and other countries have been published or obtained.

Dr. L. H. N. Cooper has continued his investigation on iron in sea-water and in plankton. In membrane filtered sea-water iron was undetectable. At such high dilutions all methods of filtration are suspect due to possible loss by adsorption, but iron as ferrous sulphate and as ferric ammonium citrate, which had been added to sea-water and filtered quickly through a membrane, was nearly quantitatively recovered. Thus there appears to be less than 1 mg. of iron in solution in each cubic metre of water, whereas the diatoms in a cubic metre, when at their maximum, contain more than 2 mg. Of iron in suspension a very variable quantity was found, ranging from 3 to 30 mg. per cubic metre in which there were no clear seasonal changes due to consumption by diatoms.

Phytoplankton in the spring contained three to four times as much iron as phosphorus, while most zooplankton—in particular ctenophores and medusæ—were relatively poor in iron.

Amongst other elements which may prove to be limiting factors in the sea is manganese, but mixed plankton catches in the spring were found to contain less than 1 mg. of manganese per thousand cubic metres of water filtered ; this is less than one-thousandth of the plankton content of phosphorus and iron.

The routine observations on the seasonal changes in inorganic phosphate in solution have been extended in connexion with the intensive plankton survey at Station L4. In the course of this survey, and of Miss Jenkin's investigations on photosynthesis by diatoms, a large number of determinations of phosphorus and a few of nitrogen have been made on plankton samples.

In order more completely to understand the phosphorus balance in the sea, information is needed as to the rate at which dead plankton organisms break down and return their phosphorus to the sea in a usable form. Known amounts of phyto- or zoo-plankton were therefore added to sea-water and the increase in dissolved inorganic phosphate followed. Autolysis of, or bacterial action upon the zooplankton brought about its very rapid breakdown and was able to liberate not only all the phosphorus in the plankton itself, but also some of the dissolved organic phosphorus originally present in the water. With phytoplankton there was an initial lag of a few days and no more than a part of the phosphorus added was set free as phosphate. Thus the animal plankton is the most effective source of the phospholytic agent which will withstand heating to 75° C., but is inactivated by ammonium fluoride.

Plankton.

The investigation of factors influencing the productivity of the sea—the supply of nutrient salts, the hydrographic conditions and the growth of diatoms—which was made during 1933 by Mr. H. W. Harvey has this year been extended, an informal collaboration with other members of the Laboratory Staff having made this possible. Observations were made at frequent intervals at a position 5 miles south-west of the Breakwater ; these included the temperature, salt, and phosphate content of the water, and the plants and the animals caught between the surface and 45 metres depth by means of a silk net having 200 meshes to the inch attached to a meter which measured the volume of sea-water passing through it. The species and numbers of the animals and plants were determined and counted by Mr. Russell and Dr. Lebour and their phosphorus content determined by Dr. Cooper. An examination of the probable error in the diatom counts has been made by Mr. Spooner. Opportunities were taken of determining the phosphorus content of diatoms when these could be separated from animal plankton. The quantity of "plant pigments" in the catches was determined and a close relation found with the numbers of diatoms present, if allowance were made for the small size of a few species.

The seasonal variation in abundance of diatoms was found to differ in detail from that found in 1933. It was again found in 1934 that the maximum population of diatoms occurring during the spring outburst only contained a fraction of the phosphorus which had been taken from the water. The abundance of diatoms showed a relation to the fluctuations in numbers of animals grazing on them, a decreased abundance of animals usually occurring at the same time as increased abundance of diatoms except in September.

From the phosphorus utilised and the phosphorus occurring in the diatom population an estimate was made of the rate of diatom growth during March, a maximum value only being obtainable. This proved similar to rates observed for several quick growing species suspended in flasks in Oslo Fjord in March, and similar to the rate of growth during the beginning of a spring outburst in Loch Striven.

The number of fæcal pellets provided an index of the intensity of grazing, which varied greatly throughout the year. It indicates that, during periods of diatom abundance, the animals eat and excrete as green fæcal pellets many times more vegetation than they need. During six weeks' scarcity of diatoms in the summer, there was no evidence of zooplankton being reduced in numbers owing to starvation, but rather the reverse.

Comparison with observations made by Marshall and Orr in Loch Striven have proved fruitful and a considerable body of evidence has accumulated which indicates that the abundance of diatoms is largely regulated by the intensity of grazing by planktonic animals in this area, and at times in other areas.

The investigation has opened up a number of questions: as, for instance, —during the first part of the year diatoms utilised at least 14 mg. phosphorus in the form of phosphate from each cubic metre of water; the diatoms and zooplankton in a cubic metre never contained more than 2 mg. P.; regeneration of phosphate started in August and was not, as far as we know, preceded by any considerable mortality of animals; it is thought that phospho-proteins and phospholipins may dissolve into the water when diatoms are eaten and only partly digested. The productivity of the sea depends largely on the rate at which phosphate is regenerated and becomes again available to the plants ; this rate deserves further investigation.

As a second instance—after six weeks or more when diatoms were sparse, the animals, although very abundant, allowed a considerable population of diatoms to be built up in September before starting to eat them in quantity, as suggested by the number of fæcal pellets per animal. It is thought that the animals had been eating much organic detritus which was abundant in the water. If the animals form a preference for their accustomed food such a preference could also account for one species of diatom succeeding another during the early summer.

The counting of the catches of zooplankton has provided data of interest as they have given for the first time figures of abundance from a known volume of water in this region. The total number of animals retained in a silk net of 200 meshes to the inch rose from a minimum of 183 in 100 litres of water in January to a maximum of 7663 in August. In comparison with this Lohmann gives monthly averages per 100 litres of sea-water for Kiel Harbour showing a minimum of 3700 in January and a maximum of 37,000 in July.

Mr. F. S. Russell has continued his observations on the seasonal occurence of different plankton animals off Plymouth. Special attention has again been given to the composition of the Sagitta population. The complete displacement of *Sagitta elegans* by *S. setosa* which took place in the autumn of 1933 continued until the spring of 1934 when a few *S. elegans* made their appearance. Throughout the remainder of the year, however, *S. setosa* has still been easily the predominant species. Representative samples have been measured and the seasonal changes in size of *S. setosa* have followed very closely those found in 1931.

Careful examination of the medusa fauna has been continued and records are accumulating to illustrate the very striking differences in its composition from year to year. These differences are especially noticeable amongst medusæ and other plankton animals occurring in the late summer and autumn months. It is interesting to record that among the medusæ five species have been found that had not been previously recorded from the Plymouth Laboratory, one of which is probably new. The free-swimming single tentacled gonophores have been hatched from the hydroid *Dicoryne* (*Heterocordyle*) *conybearei* Allman, thus confirming the observation on the reproduction of this species made by Ashworth and Ritchie some years ago at Naples.

Mr. Russell has completed two of his reports on the plankton of the Great Barrier Reef Expedition, and in this connexion he has made a number of collections simultaneously with Mr. Harvey to calibrate the catching power of his plankton net against the amount of water filtered through the Harvey meter.

Dr. M. V. Lebour has continued her investigations on living plankton with special reference to the prosobranch gastropod larvæ. Her main object is to discover which species are important as veligers in the plankton and which have little significance. Many mollusc larvæ are important economically, remaining for long periods in the free-swimming state; others are much less so, remaining only a few days or hours; while a few have no free-swimming planktonic stage at all. It is found that some of the coastal prosobranchs are very numerous in the plankton at certain times of year, notably the rissoids; one species now identified as *Rissoa sarsi* is an important food of the very young herrings in winter. *R. sarsi* has recently been found in the adult state in rock pools between tide-marks, and late larvæ from the plankton have been reared to the adult. In searching the rock pools and stones between tide-marks for rissoids in the above investigation many small gastropods new to the district have been noted and it is found that a large proportion of these have planktonic larvæ which remain in the plankton for a long time. A paper on the life history of several species of rissoids has been published in the last number of the Association's Journal. Besides the coastal forms, many gastropod larvæ of the more open water are important, notably the Lamellariidæ, Cypræidæ, Turridæ, and Eulimidæ. A paper on the larval turrids has been published in the Journal this year, one on the Echinospira larvæ (six in all) of the Lamellariidæ and Cypræidæ and another on the Eulimidæ are ready for publication. A paper on the importance of mollusc larvæ in the plankton which embodies the general work done on this subject, has been published in the *Journal du Conseil.* A large number of larvæ, hitherto unknown, have been identified and are being investigated.

Whilst searching the plankton samples for mollusc larvæ the decapod crustacean larvæ have not been neglected, and following the discovery of Dromia larvæ in the plankton last year, a paper has been published in the Proceedings of the Zoological Society of London (July) on the Life History of *Dromia vulgaris*. Some interesting facts about the larvæ of Hippolyte and Spirontocaris are being investigated showing that they are very closely related.

Mr. D. P. Wilson has been concentrating on his study of the development of the annelid worm *Branchiomma vesiculosum.*

The pelagic stages of Branchiomma are small yolky larvæ that settle on the bottom when eight or nine days old. They secrete for themselves mucus tubes in which metamorphosis takes place in about four days. During the metamorphosis the prototroch and other larval tissues form on the head, a protuberance which gradually breaks up into small pieces that are either lost or swallowed. Meanwhile the two branchial lobes that appeared anterior to the prototroch during pelagic life branch giving rise to the first branchial pinnules, which collect food and assist in building a tube of sand. After metamorphosis the branchial crown increases in complexity and the body elongates. Setigers of the thoracic type (dorsal bristles, ventral uncini) are added successively until the ninth appears. The latter shows abdominal constitution, for it at once grows dorsal uncini and ventral bristles. Thus all the adult thoracic setigers are formed before any of the abdominal type appear. There is no reorganisation of anterior segments from abdominal to thoracic constitution during normal development.

In collaboration with Mr. J. H. Day, Mr. Wilson has published in the Journal a paper describing their observations on the influence of the soil on the metamorphosis of *Scolecolepis fuliginosa* larvæ.

Breeding Experiments with Gammarus.

The experiment, started in February, 1933, by Mrs. E. W. Sexton and Miss A. R. Clark with *Gammarus chevreuxi* in order to study the origin of recessive characters in the wild, and the nature of the variations which occur, has produced a large number of young, over 12,000 in the F_1, and 20,000 in the F_2.

In sorting out the results, it became evident that the character of the wild stock had changed. The first point that was noted was the enormous increase in the number of the variations as compared with previous dredgings. Only one mutation arose in the first ten years of the work, whereas in this last experiment there occurred 12 strains with changes of retinal colour, and 9 strains with change and loss of the white accessory pigment. The next point was the difference in the *type* of variation; for instance, in the changes of retinal colour, of the 9 reds tested, 8 were found to be of the same genetical constitution as the former Stock II, and only one was distinct from any of the previously seen reds. Again, to take the change and loss of the white pigment: in 2 of the 9 strains this was proved hereditable, but the other 7 were phenotypic no-whites which, although they never developed any white pigment themselves, always gave normal-eyed offspring in all matings, whether with pure no-whites or with other similar phenotypes. Another important point was that, for the first time in twenty years, heterozygotes appeared in the F_1 from the wild.

This change in the stock may be correlated with the change in the conditions of its habitat where an alteration in the drainage of the ditches has caused considerable fluctuation in the volume, depth, salinity, and temperature of the water, and in consequence a great fluctuation in the numbers of the Gammarus population. It is suggested that with each opening of the drainage sluice gate most of the animals would be swept away in the rush of water, and if the small remnant left behind contained a variation, one would expect that the intensive interbreeding would soon establish this throughout the stock, as, in fact, it appears to have done in the case in question.

Fish and Fisheries.

With Dr. H. Lissner at the Laboratory to co-operate with Mr. E. Ford in the herring investigations, an extended programme of work could be undertaken. It was decided that it would be very profitable to obtain fuller knowledge of the relationship between the herrings taken in the different fisheries by trawl and drift-net in the waters off our south-west and west coasts, and landed at Fleetwood, Milford, Cornish ports and Plymouth. Up to the end of November about 2,750 trawled herrings have been examined in lots of 250 from landings at Fleetwood and Milford. In addition to data on length and degree of sexual maturity, otoliths have been collected for the estimation of age, and skeletons have been prepared for vertebral counts. These trawled herring will be supplemented by samples of the drift-net catches at St. Ives, Port Isaac, and Padstow, which will be similarly treated. From these drift-net fishes it is possible to take samples of scales as well as otoliths and thus to obtain an alternative estimate of age.

The drift-net fishery at Plymouth during the winter of 1933–34 failed badly. Not since the season of 1920–21 has the total weight of fish landed in December and January been so low, the motor-boat catch being almost disastrous in its poorness. Big, old fish were again predominant, fish less than 6 years old being comparatively scarce. The impression was gained that the fishermen were much in the position of the previous two seasons in having to depend upon a dwindling stock of fish growing older each year, with no recruitment of young fish to repair the losses. There can be no doubt that this recent shortage of younger fishes is a matter of considerable practical significance, but it is one for which it is at present difficult to offer an explanation. Two years ago there were some indications, admittedly slight, that the brood of young born during the season of 1929–30 was one of some promise. One might have expected this brood to have made its presence felt in the catches of last season (1933–34), but they failed to do so. It is in the coming season of 1934–35 that such a successful brood, if it exists, would show to greatest advantage in the fishery.

Mr. Ford has made progress in the study of vertebral variation among teleostean fishes to which reference was made in last year's Report. Nearly one hundred species have now been examined, and a thesis on the results is in preparation. It is shown that the taxonomic and functional significance of the variation in number and form of the different vertebral structures is of primary importance to the fishery worker engaged in biometric studies of fish populations, and that the utmost caution is needed in drawing conclusions from observed differences in vertebral character between fishes.

In continuation of his work on the Rays and Skates of the English Channel, Mr. G. A. Steven's attention has been given mainly to marking experiments and related problems in connexion with the Thornback Ray (*Raia clavata*), the chief commercial species in the western area of the English Channel. Sufficient data have now been collected to show very clearly that throughout their growing stages, until the onset of adolescence, the young of this species are remarkably non-migratory. This is well illustrated by the fact that one fish, marked on board S.S. " Salpa " and liberated where caught, was recaptured by this vessel three times in the course of a year ; i.e. *it was trawled up by the same ship in the same place no fewer than four times in twelve months.* Two months later this fish was again captured in the same place by a commercial vessel which, unfortunately, killed it. Numerous other immature fishes have been recaptured by the " Salpa " at the spot where they were liberated from a month up to two years previously, and are still at liberty, having each time been returned to the sea after measurement.

The adult Rays, however, do migrate, but an insufficient number of them have as yet been marked and recaptured to indicate clearly the extent of their wanderings. In connexion with these marking experiments reference was made in a previous report to a search for, and the discovery of, a ready means of distinguishing immature from mature females while still alive. A paper containing details of the method was published in the Association's Journal in May, 1934.

In a paper on the Ray Fishery of the western area of the English Channel published in the Journal in May, 1932, it was pointed out that the intensity with which the fishery was then being prosecuted, especially by trawlers, was a serious menace to the fish stocks and that a decrease in the intensity of trawling—by reducing the destruction of immature but growing fish—would be beneficial. Since 1932 the intensity of trawl fishing has actually greatly diminished owing to cessation of activities by most of a large fleet of Belgian motor vessels. It is therefore interesting to note that the trawlers' absence has already been reflected in greatly improved catches of larger fish by the local liners.

At the request of a firm of paint manufacturers, the " Salpa " in November last was coated with various anti-fouling compositions, supplied free of charge by the firm, with a view to obtaining accurate information on their growth-inhibiting qualities. Mr. Steven has been co-operating with the paint company in this work and has already submitted one report to them. The experiments are being continued.

Mr. Steven is also co-operating in testing the resistance to attack by marine boring organisms of various insulating substances for telegraph cables. These experiments are yet in their early stages and have not proceeded far enough to produce any results. Two short reports on the examination of samples of telegraph cable recovered from the sea have, however, been prepared. Unmistakable Teredo borings were found in one piece of gutta-percha sheathing.

Mr. F. S. Russell has continued his regular observations of the abundance of young fishes. Since his last paper published on this subject, a further period of five years has now been completed. The full analysis of the material is not yet finished, but one or two interesting points have come out. It is quite clear that the period of maximum abundance of the young of spring spawners may vary considerably from year to year. As an example, the young of the whiting, *Gadus merlangus*, appeared in maximal abundance in 1933 in the third week in April; in 1932 this point was not reached until the third week in May, and, in fact, the collections in April of that year contained hardly any young whiting. There was thus between the two years a difference of one month in the time available for feeding and growth. The post-larval stages of the bass, *Morone labrax*, have only recently been fully described by Italian workers and a short note is now in the press on the rare occurrence of the young of this species in Plymouth waters.

In August Mr. Russell spent a further short period studying tunny in the N. Sea at the invitation of Col. E. T. Peel on his yacht the "St. George." A certain number of fish were again measured and the hooks used by anglers marked. The distribution of the tunny in the waters off Scarborough was found to be different from that in 1933. In October and November two short visits were also made by Mr. Russell to Penzance to investigate the occurrence of tunny off the Cornish coast. Through the kindness of Mr. F. Taylor he was able to spend a day at sea between Mousehole and Land's End when tunny could be seen leaping out of the water all along the coast in chase of sandeels and garfish. This appearance of the tunny very close to the coast is asserted by the local fishermen to have been first noticed in 1932, the fish arriving at the end of September and staying well on into December. A general account of our knowledge of the tunny has been published by Mr. Russell in *Science Progress*.

Dr. L. E. Bayliss has continued his work on the digestive enzymes of the plaice (*Pleuronectes platessa*). Further studies have been made on the enzymes present in the wall of the gall-bladder, but it has not been possible to discover whether they reach the lumen of the intestine, and if they do reach it, by what route. The liver has been shown to contain a cathepsin, a powerful lipase, and an amylase. It is not certain whether these have any extra-cellular digestive action.

As a contribution to the study of behaviour of marine fishes, Mr. G. M. Spooner has been conducting experiments with young wrasse, the method being studied by which these fish build up habits involving the co-ordination of simple actions which at first have no connexion with one another. The learning of getting round obstructions and making detours has been chosen as a suitable subject for these investigations. The results which are being obtained are providing some definite information on the factors which are of importance in such learning, and provide data which have a bearing on problems connected with animal learning in general.

During the year a number of queries concerning the preservation of fishing gear have been answered by Dr. Atkins. The methods already tested in jars in the laboratory have been tried on nets fixed under Plymouth Pier, where the water is at times very foul and the tides strong, and also in the fish-pond at Cawsand in cleaner water. The results on the whole support the jar tests, but interesting information has been obtained. The Pier was also chosen for the exposure of several series of two-inch ropes, preserved by methods similar to those used for nets. After exposures of 6 months or a year their tensile strengths were determined in the Engineering School, Trinity College, Dublin, by Prof. J. Purser. Manilla, hemp and sisal ropes were thus treated, but the full exposures of the last named have not been completed. Results were obtained showing the very great advantages accruing from the use of certain preservatives.

The Library.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the Journal. Thanks are also due to those authors who have sent reprints of their papers, which are much appreciated. Grateful acknowledgment is also made of a valuable donation to the Library from Mr. T. H. Riches, who has presented forty-three bound volumes of pamphlets from the library of the late Sir E. Ray Lankester, to whose labours the foundation of the Marine Biological Association was so largely due.

Published Memoirs.

The following papers, the outcome of work done at the Laboratory, have been published elsewhere than in the Journal of the Association :

Cannon, H. Graham. *On the feeding mechanism of certain marine Ostracods.* Trans. Roy. Soc. Edin., Vol. LVII, 1933, pp. 739–764.

Cate, J. Ten. *Unisegmental reflexes in the dogfish.* Journ. Physiol., Vol. LXXXII, 1934, pp. 179–183.

Chrenko, F. *A list of parasitic Rhabdocœla (Turbellaria) of Plymouth.* Parasitology, Vol. XXVI, 1934, pp. 114–116.

Cooper, L. H. N. *A system of rational units for reporting nutrient salts in sea-water.* Journ. du Conseil, Vol. VIII, 1933, pp. 331–334.

Cowan, S. L. *The action of potassium and other ions on the injury potential and action current in Maia nerve.* Proc. Roy. Soc. B., Vol. CXV, 1934, pp. 216–260.

Dennell, R. *The feeding mechanism of the Cumacean Crustacean* Diastylis bradyi. Trans. Roy. Soc. Edin., Vol. LVIII, 1934, pp. 125–142.

Eggleton, M. G. *A physiological study of phosphagen in plain muscle.* Journ. Physiol., Vol. LXXXII, 1934, pp. 79–87.

E. F. *Science and State Regulation of the Sea Fisheries.* Nature, Vol. CXXXIV, 1934, pp. 593–594.

Graham, A. *The structure and relationships of Lamellibranchs possessing a cruciform muscle.* Proc. Roy. Soc. Edin., Vol. LIV, 1934, pp. 158–187.

Gurney, R. *The development of certain parasitic Copepoda of the Families Caligidæ and Clavellidæ.* Proc. Zool. Soc. Lond., 1934, pp. 177–217.

Hörstadius, Sven. *Einige Untersuchungen über die Eiweissverdauung bei Gastropoden.* Biol. Zentrallb., Bd. LIII, 1933, pp. 645–650.

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Kitching, J. A. *The physiology of contractile vacuoles. I. Osmotic relations.* Journ. Exp. Biol., Vol. XI, 1934, pp. 364–381.

Krainska, M. K. *Recherches sur le développement* d'Eupagurus prideauxi *Leach. I. Segmentation et Gastrulation.* Bull. Acad. Polon. Sci. et Lettres. Cl. Sci. Math. et Nat. B. 1934, pp. 149–165.

Lebour, M. V. *The importance of larval Mollusca in the plankton.* Journ. du Cons., Vol. VIII, 1933, pp. 335–343.

Lebour, M. V. *The life-history of* Dromia vulgaris. Proc. Zool. Soc. Lond., 1934, pp. 241–249.

Lebour, M. V. *Larval Crustacea (Decapoda and Stomatopoda). Expedition S. A. R. Prince Leopold of Belgium, Duke of Brabant, to the Extreme East* (1932). Bulletin du Musée royal d'Histoire Naturelle de Belgique, T. X, No. 8, 1934.

Lebour, M. V. *Stomatopod Larvæ.* Mémoires du Musée royal d'Histoire Naturelle de Belgique, hors série, Vol. III, 1934, fasc. 16.

Leigh-Sharpe, W. H. *A third list of parasitic Copepoda of Plymouth with Notes.* Parasitology, Vol. XXVI, 1934, pp. 112–113.

Okada, Yô K. *Régénération de la tête chez le Polychète* Myxicola æsthetica (*Clap.*). Bull. Biol., Vol. LXVIII, 1934, pp. 340–381.

Pantin, C. F. A. *On the excitation of Crustacean muscle. I.* Journ. Exp. Biol., Vol. XI, 1934, pp. 11–27.

Poole, H. H., and Atkins, W. R. G. *Some measurements of the brightness of various parts of the sky by means of a rectifier photo-electric cell.* Sci. Proc. R. Dub. Soc., Vol. XXI, 1934, pp. 1–8.

Poole, H. H., and Atkins, W. R. G. *Measurement of the current generated by a rectifier photo-electric cell.* Nature, Vol. CXXXIV, 1934, p. 810.

Poole, H. H., and Atkins, W. R. G. *The measurement of the current generated by rectifier photo-cells.* Sci. Proc. Roy. Dublin Soc., Vol. XXI, 1934, pp. 133–139, No. 13.

RUSSELL, F. S. *Marine Growths. Examination of ships.* Iron and Steel Institute. Spec. Rept. 5. Second Report of the Corrosion Committee. 1934, pp. 153–156.

RUSSELL, F. S. *The Tunny,* Thunnus thynnus, *Linnæus. An account of its distribution and biology.* Sci. Progress, No. 112, 1934, pp. 634–649.

RUSSELL, F. S. *The study of Copepods as a factor in oceanic economy.* Fifth Pacific Science Congress, 1934, pp. 2023–2034.

SEXTON, E. W., AND CLARK, A. R. *New developments in* Gammarus chevreuxi *Sexton.* Nature, Vol. CXXXIII, 1934, p. 27.

SHEN, C. J. *A comparative study of the statocysts of Eumalacostraca, with special reference to the Macrura.* Proc. Zool. Soc. Lond., 1934, pp. 534–557.

TAKATSUKI, S. *On the nature and functions of the Amœbocytes of* Ostrea edulis. Quart. Journ. Micr. Sci., Vol. LXXVI, 1934, pp. 379–431.

TUTIN, T. G. *The fungus on* Zostera marina. Nature, Vol. CXXXIV, 1934, p. 573.

WESTBROOK, M. A. Antithamnion spirographidis *Schiffner.* Journ. of Botany, 1934, pp. 65–68.

WIERSMA, C. A. G. *Vergleichende Untersuchungen über das periphere Nerven-Muskelsystem von Crustaceen.* Zeits. f. vergl. Physiol., Bd. XIX, 1933, pp. 349–385.

Finance.

The Council have again to express their thanks to the Development Commissioners for their continued support to the Plymouth Laboratory. They are grateful also for generous grants from the Fishmongers' Company (£600), the Royal Society (£50), the British Association (£50), the Physiological Society (£30), the Ray Lankester Trustees (£20), the Universities of Cambridge (£105), Oxford (£52 10s.), London (£52 10s.), Bristol (£25), Birmingham (£15 15s.), Manchester (£10 10s.), Leeds (£10 10s.), Sheffield (£5 5s.), and the Imperial College of Science and Technology (£10).

The Council has also to express its thanks to the Cornwall Sea Fisheries Committee for a grant of £25 for the year 1933–34.

Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1935–36 :—

President.

The Lord Moyne, P.C., D.S.O.

Vice-Presidents.

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The Earl of Stradbroke, K.C.M.G., C.B., C.V.O.
The Earl of Iveagh, C.B., C.M.G.
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List of Annual Subscriptions

Paid during the Year, 1st April, 1934, to 31st March, 1935

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Fisheries Survey Committee, Capetown (1934 and 1935)	2	2	0
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Dr. G. Herbert Fowler	1	1	0
C. L. Fox, Esq.	1	1	0
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	£	s.	d.
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Ian I. Hamilton, Esq.	1	1	0
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C. C. Hentschel, Esq.	1	1	0
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Office Scientifique et Technique des Pêches Maritimes, Lorient-Keroman (balance 1933 and 1934)	1	2	0
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	£	s.	d.
F. T. K. Pentelow, Esq. (1934 and 1935)	2	2	0
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Plymouth Educational Authority	1	1	0
Plymouth Public Library	1	1	0
Plymouth Proprietary Library	1	1	0
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V. Rothschild, Esq.	1	1	1
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F. S. Russell, Esq., D.S.C., D.F.C.	1	1	0
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J. E. Smith, Esq.	1	1	0
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G. M. Spooner, Esq.	1	1	0
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Mrs. N. S. Steven	1	1	0
Eric Stoneman, Esq.	1	1	0
Eric J. Tabor, Esq.	1	1	0

	£	s.	d.
Harold E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Prof. W. M. Tattersall, D.SC.	1	1	0
Prof. G. I. Taylor, F.R.S.	1	1	0
Sir Charles Howell Thomas, K.C.B., C.M.G.	1	1	0
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Prof. Salv. L. Vella	1	1	0
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Miss K. M. White	1	1	0
Dr. K. B. Williamson	1	1	0
D. P. Wilson, Esq.	1	1	0
Mrs. D. P. Wilson, PH.D.	1	1	0
R. S. Wimpenny, Esq.	1	1	0
Ronald Winckworth, Esq., F.R.G.S.	1	1	0
V. C. Wynne-Edwards, Esq.	1	1	0
Prof. C. M. Yonge, D.SC.	1	1	0
John Z. Young, Esq.	1	1	0
Total	£267	0	3

List of Composition Fees

Paid during the Year, 1st April, 1934, to 31st March, 1935.

	£	s.	d.
W. Eric Stoneman, Esq.	15	15	0
Total	£15	15	0

List of Donations to the General Fund

For the Year, 1st April, 1934, to 31st March, 1935.

	£	s.	d.
R. C. Vernon, Esq.	0	10	6
Total	£0	10	6

List of Donations towards the Aquarium Guide Printing Fund

Paid during the Year, 1st April, 1934, to 31st March, 1935.

	£	s.	d.
The Lord Moyne, P.C., D.S.O.	21	0	0
R. Gurney, Esq., D.Sc.	5	0	0
Morley H. Neale, Esq.	5	5	0
	£31	5	0

THE MARINE BIOLOGICAL ASSOCIATION

INCOME AND EXPENDITURE ACCOUNT

	£	*s.*	*d.*	£	*s.*	*d.*
To Salaries, including Institution's Contributions to Superannuation				6,899	4	1
,, Laboratory Wages, including National Insurance and Institution's Contribution to Superannuation ..				2,177	12	6
,, Depreciation of Library				489	13	7
,, Scientific Publications, *Less* Sales				540	12	6
,, Upkeep of Laboratories and Tank Rooms:						
Buildings and Machinery	296	6	3			
Electricity, Gas, Coal, Oil and Water	285	6	8			
Chemicals and Apparatus	386	17	3			
Rates, Taxes and Insurance	103	0	10			
Travelling Expenses	99	18	2			
Stationery, Postages, Telephone, Carriage and Sundries	371	4	10			
Specimens	117	12	10			
				1,660	6	10
,, Maintenance and Hire of Boats:						
Wages, including Diet Allowance, National Insurance and Casual Labour	1,617	11	3			
Coal, Water, Oil, Petrol, etc.	269	6	0			
Maintenance and Repairs with Nets, Gear and Apparatus	398	18	11			
Purchase of Material for Nets for Sale, excluding Labour	132	0	1			
Boat Hire and Collecting Expenses	13	18	7			
Insurance	280	1	10			
				2,711	16	8
,, Transfer to Depreciation Reserve Account ..				276	0	0
,, Balance being Surplus for the Year				278	10	7
				£15,033	16	9

OF THE UNITED KINGDOM.

YEAR ENDED 31st MARCH, 1935.

	£	s.	d.	£	s.	d.
By Grants:						
Ministry of Agriculture and Fisheries, Grant from Development Fund	11,521	16	6			
Fishmongers' Company	450	0	0			
British Association	50	0	0			
Royal Society	50	0	0			
Physiological Society	30	0	0	12,101	16	6
,, Subscriptions				267	0	3
,, Donations					10	6
,, Sales:						
Specimens	1,157	8	3			
Fish (*less* expenses)	82	19	0			
Nets, Gear and Hydrographical Apparatus	260	19	4	1,501	6	7
,, Table Rents (including University of Cambridge £105; Oxford £52 10s. 0d.; Bristol £25; Leeds £10 10s. 0d. Birmingham £15 15s. 0d.; Manchester £10 10s. 0d. Sheffield £5 5s. 0d.; Trustees of Ray Lankester Fund £20; Imperial College £10)				524	7	6
,, Tank Room Receipts				563	2	6
,, Interest on Investments (*less* Bank Charges)				48	12	1
,, Sale of Dr. M. V. Lebour's Book	9	10	6			
,, Sale of "Marine Fauna of Plymouth"	3	2	6	12	13	0
,, Income Tax Recoverable				14	7	10
				£15,033	16	9

THE MARINE BIOLOGICAL ASSOCIATION

BALANCE SHEET

	£	*s.*	*d.*	£	*s.*	*d.*
SUNDRY CREDITORS:						
On Open Account				205	19	7
JEWISH SCHOLARSHIP FUND:						
As at 31st March, 1934	91	4	2			
Add: Second Instalment received	125	0	0			
	216	4	2			
Less: Expenditure	156	5	0			
				59	19	2
E. T. BROWNE SPECIAL DONATION FUND:						
As at 31st March, 1934	25	8	2			
Less: Expenditure	12	4	9			
				13	3	5
DR. H. B. MOORE SPECIAL GRANT FUND:						
Grant received	229	2	5			
Less: Expenditure	229	2	5			
				–	–	–
AQUARIUM GUIDE PRINTING FUND:						
Donations received				31	5	0
NORTH CORNWALL SEAL INVESTIGATIONS:						
Grant received	25	0	0			
Less: Expenditure	25	0	0			
				–	–	–
RESERVE FOR DEPRECIATION OF BOATS AND MACHINERY:						
As at 31st March, 1934	1,032	17	11			
Add: Transfer from Income and Expenditure Account	276	0	0			
	1,308	17	11			
Less: Written Off Laboratory Apparatus, Engines and Pumps	150	0	0			
				1,158	17	11
SURPLUS:						
As at 31st March, 1934	6,037	4	1			
Add: Composition Fees	15	15	0			
Surplus for the year as per Income and Expenditure Account	278	10	7			
				6,331	9	8
				£7,800	14	9

(Signed) J. Z. YOUNG
M. H. NEALE } *Members of Council.*

TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the books of the Capital expenditure on erection of Buildings on Land held on Lease from the War Sheet is properly drawn up so as to exhibit a true and correct view of the state of the given to us and as shown by the books of the Association.

34 *and* 35 *Bedford Street,*
Plymouth. 8*th April*, 1935.

OF THE UNITED KINGDOM.

31st MARCH, 1935.

	£ s. d.	£ s. d.
Boats and Equipment, as per Valuation as estimated by the Director at 31st March, 1931		
S.S. *Salpa*	2,000 0 0	
Motor-boat	150 0 0	
Nets, Gear and General Equipment	27 0 0	
		2,177 0 0
Laboratory Apparatus, Engines and Pumps:		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost		
As at 31st March, 1934	580 2 10	
Additions during the year	243 11 1	
	823 13 11	
Less: Amount Written Off	150 0 0	
		673 13 11
Library:		
As per Valuation as estimated by the Director at 31st March, 1931, plus additions at cost less Depreciation		
As at 31st March, 1934	2,133 4 0	
Additions during the year	552 14 5	
	2,685 18 5	
Less: Depreciation	489 13 7	
		2,196 4 10
Stock of Specimens, Chemicals and Journals as estimated by the Director		325 0 0
Sundry Debtors: Sale of Specimens and Journals ..		111 18 6
Income Tax Recoverable		36 19 1
Prepayments		94 9 10
General Fund Investments at Market value as at 31st March, 1931:		
£410 14s. 8d. New Zealand 4% 1943/63	344 15 0	
£352 2s. 3d. Local Loans 3%	232 7 10	
(Market value at date £753 19s. 4d.)		577 2 10
Depreciation Fund Investments at Cost:		
£590 6s. 0d. Local Loans 3%	506 10 9	
£651 8s. 9d. Conversion Loan 3%	652 7 2	
(Market value at date £1,304 0s. 8d.)		1,158 17 11
Composition Fund Investments at Cost:		
£18 8s. 6d. Local Loans 3%	15 15 0	
£78 8s. 2d. Conversion Loan 3%	78 15 0	
(Market value at date £107 9s. 8d.)		94 10 0
Cash at Bank and in Hand:		
Coutts & Co.	128 2 4	
Lloyds Bank Limited	201 3 9	
Cash in Hand	25 11 9	
		354 17 10
		£7,800 14 9

Association and have obtained all the information and explanations we have required.
Department is excluded. Subject to this remark we are of opinion that the Balance
Association's affairs, according to the best of our information and the explanations

(Signed) Price, Waterhouse & Co.

The Journal of
Experimental Biology

(Late *The British Journal of Experimental Biology*)

EDITED BY
J. GRAY
ASSISTED BY
G. P. WELLS and E. ASHBY
Hon. Secs Society for Experimental Biology

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THE
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MARINE
BIOLOGICAL
ASSOCIATION

SECOND EDITION
1931

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OBJECTS

OF THE

Marine Biological Association

OF THE UNITED KINGDOM.

THE ASSOCIATION was founded at a Meeting called for the purpose in March, 1884, and held in the Rooms of the Royal Society of London.

Professor HUXLEY, at that time President of the Royal Society, took the chair, and amongst the speakers in support of the project were the Duke of ARGYLL, Sir LYON PLAYFAIR, Lord AVEBURY, Sir JOSEPH HOOKER, Dr. CARPENTER, Dr. GÜNTHER, Lord DALHOUSIE, Professor MOSELEY, Mr. ROMANES, and Sir E. RAY LANKESTER.

The Association owes its existence and its present satisfactory condition to a combination of scientific naturalists, and of gentlemen who, from philanthropic or practical reasons, are specially interested in the great sea fisheries of the United Kingdom. It is universally admitted that our knowledge of the habits and conditions of life of sea fishes is very small, and insufficient to enable either the practical fisherman or the Legislature to take measures calculated to ensure to the country the greatest return from the "harvest of the sea." Naturalists are, on the other hand, anxious to push further our knowledge of marine life and its conditions. Hence the Association has erected at Plymouth a thoroughly efficient Laboratory, where naturalists may study the history of marine animals and plants in general, and where researches on food-fishes and molluscs may be carried out with the best appliances.

The Laboratory and its fittings were completed in June, 1888, at a cost of some £12,000 and from that time until 1933 a sum of over £16,000 has been spent on additional buildings. Throughout this period investigations, practical and scientific, have been constantly pursued at Plymouth. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council; in addition, naturalists from England and from abroad have come to the Laboratory, to carry on their own independent researches, and have made valuable additions to zoological and botanical science, at the expense of a small rent for the use of a working table in the Laboratory and other appliances. The number of naturalists who can be employed by the Association in special investigations on fishery questions, and definitely retained for the purpose of carrying on those researches throughout the year, must depend on the funds subscribed by private individuals and public bodies for the purpose. The first charges on the revenue of the Association are the working of the sea-water circulation in the tanks, stocking the tanks with fish and feeding the latter, the payment of servants and fishermen, the maintenance of a research steamer and other collecting boats, and the salaries of the Resident Director and Staff. At the commencement of this number will be found the names of the gentlemen on the Staff.

The purpose of the Association is to aid at the same time both science and industry. It is national in character and constitution, and its affairs are conducted by a representative Council and an Honorary Treasurer, without any charge upon its funds, so that the whole of the subscriptions and donations received are devoted absolutely to the support of the Laboratory and the prosecution of researches by aid of its appliances.

TERMS OF MEMBERSHIP.

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition Fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, &c.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Plymouth.

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NOTICE.

The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for statements published in this Journal excepting when those statements are contained in an official report of the Council.